

PARASITOLOGY

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PARASITOLOGY

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15 JUL 1916



A TRI-RADIATE TAPEWORM (*ANOPLOCEPHALA*
PERFOLIATA GOEZE) FROM THE HORSE.

By F. J. MEGGITT, M.Sc.,

*Board of Agriculture and Fisheries Research Scholar,
University of Birmingham.*

(With Plate XVIII and 2 Text-figures.)

Introduction.

WHILE fixing a number of tapeworms (*Anoplocephala perfoliata* Goeze) from the small intestine of the horse, I came across a small tri-radiate specimen. This abnormality has previously been described by Neumann (2), but only briefly, and without any account of the internal anatomy. It therefore seemed advisable to compile a short account of the most salient characteristics. For the material I am indebted to Dr C. L. Boulenger, Helminthologist of this Department. I have also to thank Professor L. G. Neumann for obtaining for me a copy of his paper.

The horse from which the material was obtained had died from the cumulative effects of numerous parasites. On opening the small intestine at the post-mortem, it was found to be almost entirely filled with huge masses of the tapeworms. Only a comparatively small number were taken for subsequent fixing and examination, and it was amongst this number that the tri-radiate form was found. A close examination of the remaining tapeworms would no doubt have revealed other cases. A complete biography of all poly-radiate Cestodes hitherto described is given by Foster (1).

External Characters.

The total length of the specimen was 33 mm.; its maximum width was 6 mm., and its posterior width 3.8 mm. The number of proglottides was approximately 100. The shape of the scolex and proglottides

corresponded with the description given by Neumann. The scolex was 1.7 mm. long by 3 mm. wide. The six suckers varied slightly in size being approximately 1.35 mm. long by 1.1 mm. wide: their openings had a diameter of 0.368 mm., and their posterior lobes were 0.86 mm. long by 0.71 mm. wide. The length of the central proglottides was 0.63 mm., of the posterior 0.43 mm.

Excretory System.

The excretory system consists of longitudinal dorsal and ventral vessels, uniting in the scolex to form a definite excretory plexus. In the remainder of the strobila they extend from the neck posteriorly, one dorsal and two ventral vessels in each arm. The dorsal vessel continues practically unchanged throughout the entire course. It runs internal to the nerve and gives off a few branches which end blindly in the parenchyma. There is no trace of a commissure connecting it with any other vessels. The ventral vessels consist of two in each arm, lateral and slightly internal to the longitudinal nerve trunk. In the middle of the proglottis, each bends outwards nearly to the tip of the arm and then returns to its former position.

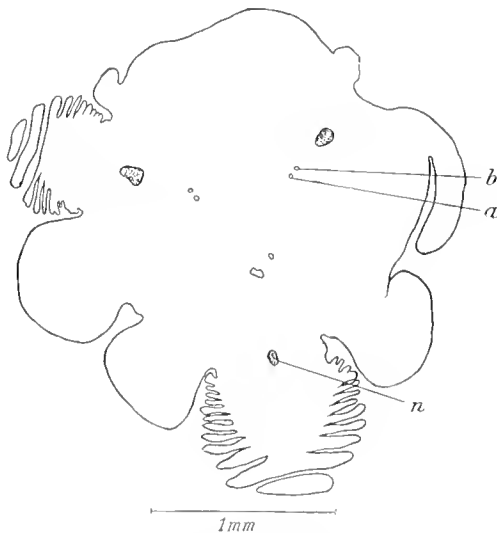


Fig. 1. Transverse section through posterior part of neck. For explanation of lettering see text.

A transverse commissure internal to the nerve connects the two vessels in the posterior part of each proglottis. In this posterior portion of the proglottis, each ventral vessel gives off one or more branches

which run internally and fuse with one another in the centre between the three arms.

As the vessels proceed anteriorly, this definite arrangement becomes lost, until just posterior to the neck, the ventral vessels are represented only by a plexus of minute branches. As the vessels pass into the neck, the excretory plexus representing the ventral vessel merges into two large transverse vessels uniting with one another just external to the dorsal vessel. Text-figure 1 presents the typical appearance here of the excretory system in a tri-radiate Cestode. From this point, the dorsal vessel (*a*) runs practically in a straight line into the scolex. The course of the ventral (*b*) is more complicated (Pl. XVIII, fig. 4). Starting lateral and slightly external to the dorsal vessel, it runs half-way to the scolex, there to bend upon itself and retrace its course to a point still more lateral to the dorsal vessel and on the same side of it as before. Again it bends round upon itself, and this time goes forwards in a straight line to the scolex where it breaks up into an excretory plexus between the sucker and the outer margin of the proglottis. The branches of this plexus reunite into a single vessel (*b'*), which runs posteriorly, increasing in size, to a point, the same distance from the dorsal vessel as the furthestmost point it reached in the first part of its course, only this time on the opposite side. From this point it again runs forward into the scolex, breaking up into an excretory plexus as before, but going to the sucker on its own side of the dorsal vessel. The posterior margins of the six suckers are thus supplied by the ventral vessels, the suckers on either side of the dorsal vessel forming a pair supplied by the corresponding ventral vessel. As before, the branches composing the plexus reunite into a large one (*b''*) which runs posteriorly half-way through the neck and then proceeds anteriorly again, external to and closely following the course of the dorsal vessel, into the scolex. With the exception of the portion before the first bend, the whole of its course lies external to the main longitudinal nerve trunk. The appearance in this part of the scolex is shown in Text-figure 2.

The excretory system in the scolex may be divided into three parts, each occupying a third of its length. Sections through the junction of two of these parts show a regular and symmetrical arrangement, sections between the junctions show only a network of vessels. In order accurately to describe these systems it is necessary to refer to each individual vessel as the majority of them have different courses.

Each of the three ventral vessels breaks up into an excretory plexus once more. The dorsal vessels on the other hand continue without a

plexus, two of them (*e, e*) converging to run side by side between two suckers (*s4, s5*) through the posterior third of the scolex (Fig. 2), the third (*a*) running by the side of another sucker (*s2*). In this part of the scolex three vessels appear suddenly to arise *de novo*. It is possible that they are formed by the collection through devious courses of the capillaries of the three ventral vessels which disappeared but this it has been found impossible to ascertain. They occupy approximately the three positions which the three vanished vessels would have occupied had they continued their courses. The new vessel between the suckers *s5, s6* crosses internally to sucker *s6*, and between suckers *s6* and *s1* divides into two (*g, h*), each branch formed being in a similar

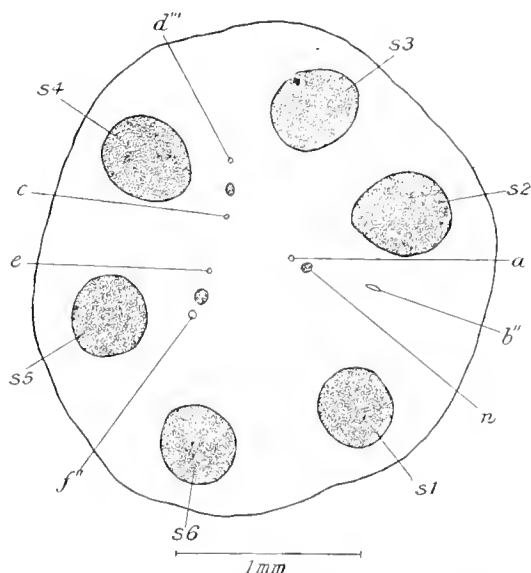


Fig. 2. Transverse section through posterior end of scolex. For explanation of lettering see text.

position to the two just mentioned (*e, e*). A further branch communicates with the new vessel appearing between suckers *s2* and *s3*. This new vessel similarly crosses sucker *s3*, but, instead of dividing into two, runs anteriorly, the other vessel of the pair being formed by the dorsal vessel (*a*) previously mentioned. At the posterior two-thirds of the scolex a section has the appearance shown in Fig. 2. The excretory system then consists essentially of six vessels (*a, d'''*, *e, e, g, h*) arranged in three pairs, each pair running side by side between two suckers, slightly to one side of the main excretory course in the neck. Of these six, three (*a, e, e*) are continuations of the dorsal vessels, the other three (*d'''*, *g, h*) probable continuations of the ventral.

Through the middle third of the scolex the courses of these six vessels are similar. Each runs directly anteriorly half-way along the length of its corresponding sucker and then turns back upon itself at an exceedingly acute angle to run posteriorly and externally as far as the point from which it started. Here it bends anteriorly again and runs between the sucker and the external limit of the scolex, slightly anteriorly to the farthest point it reached before. Arrived there it repeats its first acute-angled bend and proceeds anteriorly again, almost in a straight line with its course before the loops; often the two are connected by small capillaries. During its whole course minute branches are given off to the sucker, and others establish communication between the parallel portions. In the anterior third of the scolex the excretory system shows no definite arrangement, it forms an immense and intricate plexus (Fig. 5, only the larger branches are shown) the branches of which anastomose with one another and sub-divide to such an extent as to render analysis impossible.

The two vessels of each pair are first united by a transverse commissure (*i.e.*) each afterwards splitting up into one or more smaller vessels which combining with similar branches from the other pairs form the plexus. The labyrinth formed by one pair of excretory vessels tends to remain separate from that formed by another pair, and only communicates with it by large and definite vessels. Such communications (*i.e.*) are usually three on each side, but their position varies irregularly.

Nervous System.

The nervous system consists of three longitudinal nerve trunks running the whole length of the body. In the scolex they converge and at the posterior level of the suckers fuse to form a central mass. From this six nerves are sent out, one to each sucker. Numerous other branches are also given off. Owing to having only one series of sections and the consequent necessity of using a general stain, it was found impossible to follow out the nervous system with any clearness beyond this point.

Genital Organs.

The genital organs may be divided into two groups. The first occurs in the space formed by the junction of the three arms, with the female genital organs lying near the external parenchyma at the junction of arms 2 and 3, and the male organs occupying approximately the centre of the space. The occurrence of this group is very spasmodic,

not corresponding to the external segmentation but occurring much more frequently. The arrangement of their duets is irregular in the extreme. The genital organs of the second group lie in arm 1 and in their occurrence correspond with the external segmentation. The courses of their duets are quite normal and the general arrangement agrees very well with that described for this species. The male and female duets open to the exterior in the normal manner.

In young segments the three arms are all parenchymatous with no spaces, the genital organs being embedded in the parenchyma. More posteriorly this begins to be less compact and a space forms at the point of intersection of three lines drawn down the centre of each arm parallel to its sides. This space increases in diameter until it becomes approximately circular, with the above-mentioned point of intersection for its centre, and occupies almost the whole of the space formed by the junction of the three arms (Fig. 7, *c. sp.*). In this space lie the chief male genital ducts of the first group, cirrus, vesiculae seminales, cirrus-pouch, etc., supported by thin strands of tissue which fix them to the sides. Posteriorly this space is practically continuous through the remainder of the strobila and forms a ready means of communication between the different proglottides. Into it, close together, open the male and female genital ducts. In the anterior part of the strobila where there is no central space, its place being occupied by a compact block of parenchyma, these genital ducts have no outlet and end blindly in the parenchyma: it is not until this space is developed that the duets become functional.

It is obvious that for the genital organs of the first group there can be no cross-fertilisation, self-fertilisation must be the natural order of things. The male and female duets opening side by side into the central space would make it easy for the cirrus to fertilise the vagina of the same proglottis. This need not necessarily be the case though. The central space passing through the matrix segments would afford a ready means of communication between the different proglottides.

Spermatozoa shed into this passage would wander through it and enter any one of several vaginae: there could therefore be cross-fertilisation between two proglottides. It is certain that fertilisation actually occurs. Both male and female organs are well-developed, producing mature and apparently normal ova and spermatozoa, and mature and developing eggs are present in the uterus.

Male Organs.

The male organs of the first group present a peculiarity so far not recorded. They are usually arranged in pairs, each pair having a common opening into the central space. The vesicula seminalis and vas deferens of the more anterior of the pair run posteriorly and those of the more posterior run anteriorly, the cirri of both opening into a common duct which then opens into the central space. This arrangement is occasionally varied by segments in which the male ducts do not join either those of the preceding nor those of the succeeding segment: in that case the ducts are always incomplete, a vesicula seminalis being present, but no cirrus and no opening.

The common duct (Fig. 6, *c.d.*) of each pair of male genital organs is a short tube, enlarged at its outer end into a small sinus (*g.s.*). From this it runs towards arm 2, and after a short course reaches the point where the two cirri open into it, there ending blindly. The arrangement of the other ducts in each of the pair is the same, if allowance be made for the difference caused by one being situated anteriorly and one posteriorly. The more anterior cirrus (Fig. 3) runs slightly anteriorly and towards the junction of arms 1 and 2 until it reaches the lateral limit of the central space. Here it bends round and opens into a large vesicula seminalis (*a.v.s.*). This runs posteriorly and retraces the course of the cirrus nearly to the lateral limit between arms 1 and 3 of the central space where it contracts to an exceedingly narrow tube passing through a thick highly muscular cylindrical mass (*c.s.*) 0.15 mm. in transverse diameter. The other cirrus meanwhile has run in a similar manner first posteriorly and then anteriorly, opening into a vesicula seminalis (*p.v.s.*) which also opens into this muscular mass.

At the posterior and anterior limits respectively in this organ the two ducts often fuse. This is the last point where they come into contact with each other. From here, one runs anteriorly and one posteriorly for some distance through this muscular organ, finally to open into a second vesicula seminalis (*a.'v.'s.'*, *p.'v.'s.'*). From a comparison of transverse sections of the tri-radiate Cestode with similar sections of a normal one, I am inclined to think that the muscular organ (*c.s.*) just referred to is the extreme inner end of the cirrus sac. It is however much thicker and much more muscular than in normal specimens and usually is not continued round the cirrus and first vesicula seminalis. Sometimes the two latter are surrounded by a membrane but usually they are free. On the other hand, in normal specimens there

is an internal vesicula seminalis in the cirrus sac separated by a short narrow duct from an external vesicula seminalis outside the cirrus sac, the part of the cirrus sac through which this duct passes being much thickened. This corresponds with what occurs in the tri-radiate Cestode. On that hypothesis, the vesicula seminalis (*a.v.s.*, *p.v.s.*) first mentioned is the internal one inside the cirrus sac, the second (*a.'v.'s.'*, *p.'v.'s.'*) is the external one outside the cirrus sac, and the muscular organ (*c.s.*) is the only persistent, although abnormal, part of the cirrus sac through which the connecting duct between the two vesiculae seminalae passes.

The course of the external vesicula seminalis (Fig. 3, *a.'v.'s.'*, Fig. 6, *p.'v.'s.'*) is very irregular. It always lies at the base of arm 1 or arm 3, and, after a more or less convoluted course, narrows to form a vas deferens (Fig. 3, *a.v.d.*), dividing and sub-dividing into numerous minute vasa efferentia. These intertwine with each other considerably, but finally lead to the small spherical testes. The latter lie in three separate groups in the parenchyma surrounding the central space, one group at the base of each of the three arms, extending along as far as, or occasionally beyond, the dorsal excretory vessel. The groups are not distinct from each other, but are only local aggregations upon a continuous chain of testes surrounding the central space on three sides, the fourth and free side being that facing the ovary.

The testes appear very quickly after the scolex and in quite young segments are well-developed: in those segments, vasa efferentia and vas deferens are also present. In older segments the testes commence to degenerate and in proportion as the male ducts develop tend to disappear. The spermatozoa are formed and are ejected into the vasa efferentia before the male ducts have completed their development, so that in young proglottides with testes the vas deferens is empty, but in older segments without testes it is filled with spermatozoa. As the male ducts are completed towards the central space, the spermatozoa move along them as far as the internal vesicula seminalis where they are usually stored. The development of the outer portions of the male ducts is at first apparently quite normal, each set being quite distinct from its neighbour: as development proceeds however, each set approaches closer to its fellow, fusion eventually taking place when the internal vesicula seminalis is filled with spermatozoa ready for copulation. The common opening is then formed. This development accounts for the peculiarity before mentioned of the male ducts of a proglottis being always incomplete, possessing neither cirrus nor opening, when

they do not fuse with those of a neighbouring segment. No fusion of ducts having taken place, the development is arrested at that stage and no opening not cirrus can be developed.

Female Organs.

The female organs of the second group present no peculiarities worth mentioning. In the first group the ovary (Figs. 7 and 8, *ov.*) has the form of an arc with a plane side following the margin of the proglottis, the other side sending out at right angles numerous lobes which stretch half-way across the arm. The lateral ends of the ovary are at the limit of the inner two-thirds of the length of the arm, i.e. from arm 2 to arm 3 the ovary occupies exactly the inner third, following the margin. Its plane border is exceptionally close to the musculature, touching it in some places. At its exact mid-point on the lobed (i.e. inner) side is the oöclapt (*oöc.*). On either side of this, for a short distance, the ovary is only a simple unlobed band, the lobes only occurring lateral to all female ducts and glands with the exception of the uterus. In structure, the ovary corresponds to the usual *Anoplocephala* type.

The vitelline gland (*y.g.*) is two-lobed, lying internal and slightly posterior to the ovary. Externally it nearly touches the band part of the ovary, laterally it stretches as far as the lobes, filling the break in their line. Posteriorly its two lobes communicate by a narrow bridge from which proceeds the vitelline duct (*y.d.*). In the hollow of the "U" thus formed lie the oviduct and shell-gland.

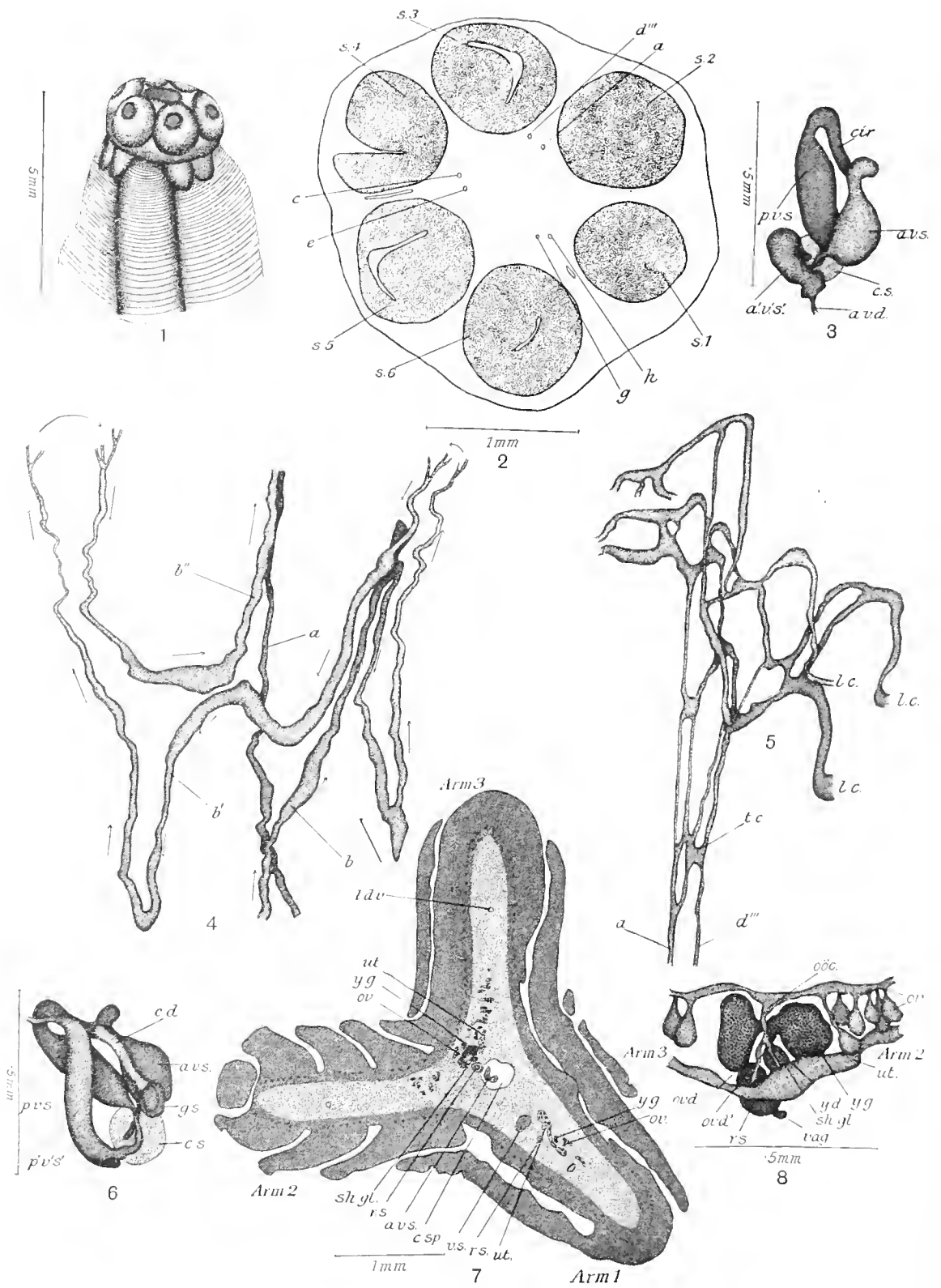
The receptaculum seminis (*r.s.*) is rather variable in position. Usually it lies slightly towards the arm 3 side of the exact centre, with its inner end pointing towards the ovary through the U-shaped hollow of the vitelline gland and its outer end to the corresponding position at the junction of arms 1 and 3. Occasionally it swings round upon its inner (oviducal) end until its vaginal end points towards the corresponding position at the junction of arms 1 and 2. In shape it is rather elongated and slightly bent, with the concavity directed towards the arm 3 side of the ovary.

The shell-gland (*sh.gl.*) has the usual shape, is rather compact and surrounds a small oötype. It is usually on the arm 2 side of the receptaculum seminis, near and anterior to its oviducal end, but it may also be on the arm 3 side. This variability bears no relation to that of the receptaculum seminis. The shell-gland is partly enclosed between the two lobes of the vitelline gland.

The courses taken by the female ducts are irregular in the extreme. A typical course and arrangement can be distinguished, but this is liable to almost any variation. The oviduct (*ovd.*) joining the ovary and receptaculum seminis runs straight from the inner end of the latter towards the former: after crossing the vitelline bridge it bends towards arm 2, then runs for a short distance anteriorly or posteriorly and bends back again to open into the ovary through a small but pronounced oöclapt (*oöc.*). The part of the oviduct (*ovd.*.) leading to the shell-gland separates from that leading to the ovary at any point before the vitelline bridge. It normally bends towards arm 2 and, after several variable curves, opens into the oötype where it receives the vitelline duct (*y.d.*). In one dubious case, the vitelline duct apparently opened into the oviduct after it had left the oötype. After leaving the oötype, the oviduct runs towards the middle point of the junction of arms 1 and 2 for a short distance, and then curves round to run in the opposite direction close to the ovarian side of the receptaculum seminis. It finally turns in the direction of the ovary and opens into the uterus (*ut.*). This is a rather narrow, little-branched tube extending nearly to the dorsal excretory vessels of arms 2 and 3, following the outline of the ovary.

In its opening to the central space, the receptaculum seminis is exceedingly peculiar and variable. The simplest case is where it opens into a vagina, which, after a short bend in any direction, opens into the central space. A more usual arrangement is for several receptaculæ seminae to communicate with each other first. Of the series, the most anterior opens into a short narrow duct leading directly posteriorly and opening into what would normally be the external end of the succeeding receptaculum seminis. This again communicates by means of a similar duct with the next receptaculum seminalis, and so on until the end of the series is reached, the last receptaculum seminalis communicating only with its predecessor and its own female organs. In one special case, a receptaculum seminis was absent, the connecting duct opening directly into the ovary. About half-way along the series of short ducts connecting the whole series of receptaculæ seminae (usually three or four) is another similar duct, opening at one end into the connecting ducts and at the other into the central space, fairly close to the opening of the cirrus.





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- (1) FOSTER, W. D. (1915). Two New Cases of Polyradiate Cestodes, with a Summary of the Cases already known. *Journ. of Parasit.* II. 7-19.
- (2) NEUMANN, L. G. (1890). A propos d'un Taenia trièdre de l'espèce *Taenia perfoliata* Goeze. *Revue vétér.* xv. 478.

EXPLANATION OF PLATE XVIII.

REFERENCE LETTERS.

a.v.d. anterior vas deferens; *a.v.s.* outer anterior vesicula seminalis; *a.'v.'s.'* inner anterior vesicula seminalis; *c.d.* common male duct; *cir.* cirrus; *c.s.* cirrus sac; *c.sp.* central space; *g.s.* genital sinus; *l.d.v.* longitudinal dorsal excretory vessel; *oöc.* oöclapt; *ov.* ovary; *ovd.* oviduct; *p.v.s.* outer posterior vesicula seminalis; *p.'v.'s.'* inner posterior vesicula seminalis; *r.s.* receptaculum seminis; *s.* sucker; *sh.gl.* shell-gland; *ut* uterus; *vag.* vagina; *y.d.* vitelline duct; *y.g.* vitelline gland.

a, b, b', b'', c, d''', e, g, h, l.e., t.e. (for explanation see text).

- Fig. 1. Scolex.
- Fig. 2. Transverse section at posterior third of scolex.
- Fig. 3. Male genital ducts, seen anteriorly.
- Fig. 4. Excretory system in neck.
- Fig. 5. Excretory system in anterior third of scolex.
- Fig. 6. Male genital ducts, seen posteriorly.
- Fig. 7. Transverse section of a proglottis.
- Fig. 8. Female genital ducts.

A CONTRIBUTION TO THE KNOWLEDGE OF THE TAPEWORMS OF FOWLS AND OF SPARROWS.

By F. J. MEGGITT, M.Sc.,

*Board of Agriculture and Fisheries Research Scholar,
University of Birmingham.*

(With Plates XIX–XXI and 1 Text-figure.)

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Introduction.

THE present paper contains the results, other than those already published, of work done in the Department of Agricultural Zoology at the Birmingham University upon the tapeworms of birds. At the commencement, a little over two years ago, the aim was to make a complete investigation of the Cestodes of British birds, both from the standpoint of anatomy and also of life-history, since, as far as I am aware, there exists no adequate description of them. It was found impossible to obtain a regular supply of any one species of tapeworm, hence the work upon one particular species could only be carried on spasmodically. The results, having to wait upon the occurrence of the material, are necessarily incomplete. Circumstances having made it necessary temporarily to postpone the work, it was considered advisable to write up and publish the results so far obtained.

I should wish here to express my indebtedness to Professor Gamble for the help he has given me during this period, more especially in the solution of problems arising from the life-history work.

With reference to the effect of Cestodes upon their host, very little can be added to what has already been published (8). The most pronounced symptom has always been the very marked emaciation shown by the birds (Pl. XXI, figs. 20-22). As a rule, flesh was almost entirely absent from the breast and the legs were thin and withered. The skin was invariably very dry and scaly, peeling off in large flakes: often feathers were absent from the breast, neck, etc. The alimentary canal has always been rather suffused with blood and containing a certain amount of mucus, but nothing like the appearances quoted by Stiles (12) have been observed. There has never been the least alteration in the appetite, neither has there been shown a marked desire for water. Altogether, with the exception of the emaciation, the birds seemed quite normal. It is very probable however that the retarded growth of many pullets and cockerels is due in many cases to infection by Cestodes. From an economic point of view this effect is a very serious one and deserves to be tested thoroughly. Several cases lately have been observed in which the presence of the parasite has seemed to check egg-laying, but no definite conclusion has yet been reached. The cause of this cessation seemed to be due rather to environmental influences than to the parasites.

Davainea dubius nov. spec.

From time to time, in examining the intestines of fowls sent to me, I have come across small Cestodes which I at first identified as *Davainea proglottina* Davaine. Recently however, the abnormal length of some specimens I found in a very badly infected fowl aroused my attention, and, examining them closely, I discovered many points of difference between them and *D. proglottina*. Previous specimens preserved and identified as the latter species I re-examined and usually found the same differences. It therefore seems to me probable, either that two species have been confused under the same name or that there are serious discrepancies in Davaine's diagnosis. In either case it appeared necessary to compile a short description of the form found.

Occurrence. Warwickshire, Worcestershire, Staffordshire, Shropshire, Gloucestershire and Lincolnshire.

External Characters. The total length of the new form averages 3.3 mm. and its greatest width 0.63 mm.; the largest specimens found

measured 4.048 mm. long by 0.807 mm. broad. The head is very like that of *D. proglottina*. It is provided with a slightly muscular spheric rostellum 0.041 mm. in diameter, its anterior extremity capable of invagination upon itself: it is situated at the bottom of a shallow apical depression of the scolex and lies anterior to the suckers. Usually it is extended, protruding half-way from the apex of the scolex. It is armed with 50–60 hooks (Pl. XIX, fig. 5) of the characteristic *Davainea* type arranged in two rows. The hooks of each row alternate with one another, the distance between the transverse level of the head of a hook of one row and that of a hook of the other being so slight as to cause the hooks to appear in a single row. The hooks differ in size, those of one row being 0.0071 mm. long, those of the other 0.0084. This rostellum differs from that described by Blanchard (1) for *D. proglottina* in that it is spherical instead of hemispherical (although this may only be due to muscular causes), the hooks number 60 at the most instead of 95, and the “large fossé circulaire entre le rostre et l’infundibulum” does not exist in this case. The four suckers are very shallow and are armed with approximately 4–6 concentric rows of hooks whose lengths vary from 0.0052 mm. to 0.0086 mm.: there is a tendency for the number of hooks to be less upon the posterior border than upon the anterior. A short neck is present. The strobila (Pl. XIX, fig. 1) is usually composed of seven proglottides, but as many as nine may be present. The first two are broader than long, the next three quadrangular, and the succeeding ones longer than broad: the terminal proglottis may be as much as $2\frac{1}{2}$ –3 times longer than broad. There is no sign of a division between the proglottides as figured for *D. proglottina*, nor of the peculiar concavity of the angles. (Compare Text-figure 1 with Pl. XIX, fig. 1.)

Attachment of Scolex. The scolex is only attached to the free surface of the duodenal mucosa (Pl. XXI, fig. 23); it sometimes nearly reaches

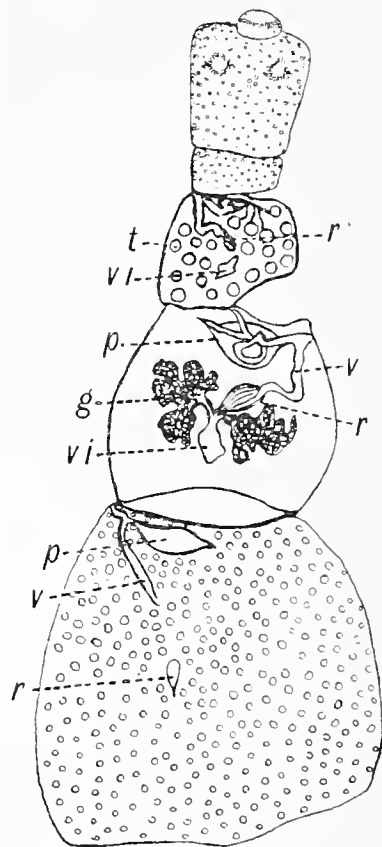


Fig. 1. *Davainea proglottina* (after Blanchard). $\times 95$.

the submucosa, but, unlike *D. echinobothrida*, never penetrates it. It is nearly always in an extended condition, the short neck and first proglottides being considerably extended. The head is thrust between the villi until it touches the mucosa, into which it burrows to a greater or lesser degree: the epithelial covering of the villi touching the worm is entirely stripped off, so that in a transverse section the worm seems to be lying in a small tube. There is a slight thickening and coalescence of the villi near the point of attachment. In the majority of cases the rostellum is retracted, its hooks are withdrawn, and it seems to take no part in the fixation of the worm to the duodenal wall. Sometimes the hooks can be seen to be embedded in fragments of tissue, but these cases are not frequent. It is possible that this contracted condition is due to the action of the fixative, or to contraction of the worm upon the death of the fowl and the opening of the alimentary canal. In a few cases the apical cavity formed by the retraction of the rostellum was filled with mucus which attached the worm firmly to the wall of the duodenum. The suckers appear to take the chief part in the attachment of the worm. The 4-6 concentric rings of hooks with which they are armed are embedded firmly in the villi nearest them, so firmly that they are usually torn from the suckers during sectioning. This species is usually present in many hundreds in the duodenum and the damage done to the wall must consequently be very great. The endodermal cells would be stripped off a large part of its surface and absorption of food proportionally hindered, if not absolutely prevented. There is also a certain amount of bleeding from the torn surface, resulting in the formation of strings of mucus and blood-clots: these would not usually be sufficiently large or numerous to attract attention, but in very bad cases would cause the faeces to have the bloody appearance mentioned by Zürn (13). Such cases I have not yet observed.

Musculature. The musculature consists of longitudinal and transverse muscles lying just under the sub-cuticular layer. The longitudinal muscles are comparatively strong, considering the size of the Cestode, and run from end to end of the proglottis in single strands. In the anterior portion of the strobila these strands are continuous from segment to segment and extend into the scolex: they ultimately end on the inner surface of the rostellum and suckers. Posteriorly they are interrupted between the proglottides. The transverse muscles consist of much smaller strands, connecting the various strands of the longitudinal muscles. They are best developed in the scolex between the suckers. At both extremities of each proglottis is a more or less

continuous layer of transverse and dorso-ventral museles: between each proglottis and its neighbour therefore is a small thin parenchymatous space, bounded anteriorly and posteriorly by these musele layers. These plates in the anterior portion of the strobilus are more or less interrupted by the strands of the longitudinal museles, and in themselves are defective, having numerous large spaces between their constituent museles. More posteriorly these defects disappear and the longitudinal museles lose their continuity. In the segments ready to be detached, the process reaches its conclusion. The plates are formed by an uninterrupted musele layer in which the distinction between transverse and dorso-ventral museles has nearly disappeared, the parenchyma in the enclosed space degenerating. When the proglottis is detached these plates contract, drawing its edges together.

Excretory System. The excretory system in this form is so minute that little of its general plan could be ascertained. There are the usual four longitudinal excretory vessels, the ventral of which soon disappear, and their transverse commissures. Round the anterior part of the rostellum is a circular commissure into which the longitudinal excretory vessels open, and just posterior to it is a second, connecting the four vessels. Numerous fine branches radiate from this and the longitudinal vessels, some of them apparently leading to the suckers although this could not be definitely ascertained. There is evidence of an elaborate and definite system in the scolex, but owing to gaps in the vessels and to their exceptionally small size, it was found impossible to unravel it.

Nervous System. In the body, the nervous system consists of the usual two main longitudinal nerve trunks and their numerous branches. The main longitudinal nerves pass unaltered through the neck. Just posterior to the suckers each divides into two, the two branches of each side merging after a short course into a central nerve mass or "brain." This latter lies in the centre of the proglottis just posterior to the hinder border of the suckers. It is a flattened irregular six-pointed mass with a small antero-posterior diameter, the longitudinal nerves entering it some little distance from its lateral extremities. Of the six points, the two dorsal and the two ventral give rise to nerves leading straight to the posterior borders of their respective suckers. The nerves from the two lateral points run anteriorly as far as the anterior border of the suckers and there join a circular commissure. The commissure touches the inner borders of the suckers and supplies them with numerous nerves: in the spaces between the suckers it bends to the exterior, and half-way between them expands into a small ganglion from which nerves

run, slightly anteriorly, across the segment to the posterior border of the rostellum.

Male Organs. The male organs first appear as an "Anlage" in the second segment and are not completely developed until the third (Pl. XIX, fig. 2). The testes (*t.*) are 12-15 in number. They are irregular oval bodies, lying closely packed together at the posterior extremity of the proglottis: they have no definite arrangement. The vasa efferentia combine together at about the level of the shell-gland to form a dorsal vas deferens. This runs anteriorly to the border of the proglottis, bends and twists to form an elaborate coil, and then opens into the cirrus-sac. There is no vesicular seminalis, the coils of the vas deferens taking its place. The cirrus-sac lies transversely across the proglottis, reaching two-thirds of the way across. In it the vas deferens twists elaborately, ultimately ending in a long cirrus armed with fine spines. The opening of the cirrus is at the inner end of a long genital sinus, making an angle of 45° with the side of the proglottis, and opening to the exterior almost at the anterior corner of the segment. The position of the genital pore thus formed alternates regularly from side to side. The cirrus-sac generally persists in the last proglottis, but the testes disappear as soon as the eggs begin to be distributed in the parenchyma. In certain cases self-fertilization occurs. In three stained specimens the cirrus is inserted into the vagina (Pl. XIX, fig. 3), this being also seen in living forms, and many times it is thrust into the genital sinus without being turned to the exterior. On the other hand, it is often protruding out of the genital sinus, indicating cross-fertilization, and this method seems to be more usual than the other.

Female Organs. The female organs (Pl. XIX, fig. 2) conform to the usual *Davainea* type. They are first developed in the third segment, in which the "Anlagen" of vagina and receptaculum seminis can be seen. In the following segment they are completely developed and are functional. The uterus is not developed until the fifth proglottis and only lasts until the sixth. In that proglottis, the receptaculum seminis and vagina alone of the female organs remain, and the eggs begin to pass into the parenchyma. The mature eggs are to be found in the seventh segment, although they may sometimes be present in the sixth. In the centre of the proglottis and with its long axis directed antero-posteriorly is a large oval receptaculum seminis (*r.s.*) filled with spermatozoa, and communicating with the exterior by means of a much-coiled vagina (*v.*): this latter opens into the genital sinus just posterior to the cirrus. At the posterior extremity of the receptaculum

seminis and on its pore side a large duct arises and leads into the oviduct. The oviduct runs dorso-ventrally near the centre of the proglottis, leading ventrally to an ovary (*ov.*) similar to that described by Blanchard, and having its cavity divided by septa into numerous incomplete compartments. Dorsally it passes to the shell-gland, receiving there the duct from a ventral, roughly quadrilateral, vitelline gland (*v.g.*). From the shell-gland it runs anteriorly to the extremity of the receptaculum seminis, there to pass dorso-ventrally across the proglottis and open on the ventral side into a small uterus. It passes the receptaculum on its pore side. The uterus is a small simple sac on the ventral surface of the proglottis, between the anterior border and the ovary. From the latter it is only separated by a few strands of parenchymal tissue which break down upon sectioning, thus causing the two spaces to seem in communication with each other. Only by careful examination of the ducts can it be distinguished from the many cavities of the ovary. It is not persistent, being present only in two proglottides. By about the sixth segment its walls disintegrate and the eggs become scattered throughout the parenchyma. These in the following proglottis are enclosed singly in large spherical cavities (Pl. XIX, fig. 4) the walls of which, as Blanchard pointed out in *D. proglottina*, correspond to the outer egg-membrane. The egg is of the usual Cestode type, with a diameter of 0.033 mm.; the diameter of the onchosphere is 0.023 mm.

Conclusion. As can be seen from the above account, the form described presents many differences from allied species. Of the avian species of *Davainca* only eight have armed suckers and alternating genital pores: these are *D. circumcincta* (12), *D. circumvallata* (12), *D. crassula* (3), *D. echinobothrida* (10), *D. hertwigi* (9), *D. insignis* (12), *D. proglottina* (1), and *D. urogalli* (11). Of these *D. circumcincta* and *D. insignis* are too inadequately described to enable them to be distinguished. The remainder, with the exception of *D. proglottina*, can be separated from the form now under discussion by the position of the genital pore being half-way along the lateral margin instead of at the extreme anterior corner, this being a character not liable to variation. *D. proglottina* is therefore the species most closely allied to the new form. There are considerable differences between the two; these are given in Table I.

In addition the female organs of the new form persist in segments five, six and seven, while these segments are not present in *D. proglottina*. It is obvious therefore that the two forms constitute two different species. A variety of *D. proglottina*, *D. proglottina* var. *dubla-*

nensis Kowal. (5) has previously been recorded, a description of which I have not yet been able to obtain. Should this variety prove to be the same as the form under discussion, this name would of course have priority. In the meantime I propose the name *D. dubius* provisionally for the new form.

TABLE I.

<i>D. proglottina</i>	5 proglottides present	95 rostellar hooks ...	1 row of hooks upon suckers
New form ...	9 proglottides present	50-60 rostellar hooks	4-6 rows of hooks upon suckers
<i>D. proglottina</i>	No attached proglottides longer than broad	Second segment contains vitelline gland and functional male organs	
New form ...	4 attached proglottides longer than broad	Second segment contains only the "Anlage" of the male organs	
<i>D. proglottina</i>	Third segment contains functional female organs. Only cirrus-sac remains of the male organs	Fourth segment contains only eggs	
New form ...	Third segment contains functional male organs and "Anlagen" of vagina and receptaculum seminis	Fourth segment contains functional female organs and testes. Eggs not mature until seventh segment	
<i>D. proglottina</i>	Testes "disposées dans les parties latérales de l'anneau*." A vesicular seminalis absent	"La glande coquillière n'est pas apparente, non plus que l'utérus"	
New form ...	Testes in two rows along the posterior margin of the proglottis. Vesicular seminalis absent	Shell-gland present. Uterus present although not persistent	

Specific Diagnosis. Length of strobila 3 mm., width 0.6 mm. Head, 0.16-0.165 mm. long by 0.13 mm. wide, with retractile rostellum, 0.041 mm. diameter, armed with two rows of 30 hooks each, those in one row being 71 μ long, in the other 84. Suckers shallow, 0.045 mm. diameter, armed with 4-6 rows of hooks 52-86 μ long. Neck short. Number of proglottides usually seven. Genital pores regularly alternate, at the anterior angle of the proglottis. Testes 12-15, in two rows along

* In the figure of the second segment given by Blanchard (1) the testes are represented as being uniformly distributed throughout the proglottis. See Text-figure 1.

the posterior margin of the proglottis. Vesicula seminalis absent. Cirrus armed with fine spines. Female organs as in *D. proglottina* with the exception of their later development. Shell-gland present. Uterus developed but not persistent. Eggs in parenchyma, not in egg-capsules. Diameter of egg 0.033 mm., of oncosphere 0.023 mm.

Life-History. Experiments have been made with a view to working out the life-history of this species, but so far have only given negative results. According to Grassi and Rovelli⁽⁴⁾, the intermediate hosts of *D. proglottina* are the slugs *Limax cinereus* Lister, *L. agrestis* Linn., and *L. variegatus* Drap. It was thought therefore that as *D. proglottina* appeared to be the nearest species to *D. dubius*, slugs would probably be the intermediate hosts of the latter. Feeding experiments were therefore made with as many varieties of slugs as could be obtained. The chief obstacle was the heavy mortality amongst them when kept in captivity. The slugs employed were kept in large earthenware pots, the bottoms of which were covered with moist earth upon which stones were placed. In order to prevent them from escaping, fine muslin was placed across the top of the pot. The whole was then placed in total darkness. Cabbage and potato were found to be the best foods. Yet in spite of all care culture after culture died off, and often it was found that when one came to record the experiment the slugs were already dead. That slugs undoubtedly eat tapeworms was proved by Miss Lebour⁽⁶⁾ and by eggs being found in their intestines. Dissections and sections however never showed the slightest trace of developing cysticercoids.

Altogether 5 *Arion ater* L., 6 *A. hortensis* Fer., 18 *A. circumscriptus* John., and 45 *Agriolimax agrestis* L. were fed and examined, the time elapsing between the first date of feeding and the dissection varying from 10 to 35 days. These slugs were the only ones found in the fields, and of these only *Arion circumscriptus* and *Agriolimax agrestis* were common. It therefore seems to indicate that slugs are not the intermediate hosts. In the case of life-histories, however, a negative result should only be accepted with suspicion since there are so many causes operating unfavourably. In the first place it is not possible in dealing with such small forms to ascertain before use that the tapeworm eggs are mature and fertilised. Next it cannot be proved that all the slugs, or that even a small minority, will eat the eggs, in spite of the latter being smeared over the food. Again, considering the heavy mortality, it is probable that the infected slugs would be amongst those first to die and would consequently be overlooked. And, lastly,

the necessarily artificial conditions under which the infected animals must be kept may quite conceivably react on their health to such an extent as to render them an impossible host for any normal parasite. It can therefore be seen that the result obtained cannot by any means be considered as conclusive, but that many more experiments are necessary before it can be accepted.

Davainea cesticillus Molin.

Occurrence. Warwickshire. I have only found this species three times. One fowl contained three specimens and numerous *D. dubius*, and the other two only contained one specimen each.

Attachment of Scolex. The apex of the rostellum (Pl. XXI, fig. 24) is inserted into the centre of one of the intestinal villi as far as the hooks, pushing the tissue before it. As soon as the hooks touch the villus they insert themselves into its walls. The rostellum is then retracted to its fullest extent, and at this stage has a small terminal depression. Degeneration of the intestinal tissue around the apex of the rostellum next begins, a small space communicating with a capillary being formed. From this stage onwards the intestine becomes highly vascular, the villi becoming so suffused with blood as to have a distinct reddish tinge when seen with the naked eye. In the cavity of the villus around the rostellum can be seen fragments of degenerating intestinal tissue and numerous blood corpuscles, some entering the small terminal depression and all clustering closely round the apex. In all cases the nuclei of the intestinal cells persist longest, the protoplasm on the other hand is absorbed rapidly. Attachment is by the rostellum only, for although sometimes degenerating tissue can be seen in the cavity of the suckers, this is merely accidental, the suckers having no part in the attachment.

The highly vascular state of the intestine and the intimate connection between the Cestode and the intestinal capillaries seem to indicate that the parasite obtains part, at least, of its food from the blood.

Excretory System. The excretory system is almost identical with that of *D. dubius*, consisting of four longitudinal vessels and two circular commissures connecting them in the anterior part of the scolex. From the more anterior commissure, one branch at least is given off to each sucker.

Genital Organs. Investigations of the genital organs fully confirm Ransom's (10) account.

Amoebotaenia sphenoides von Linstow.

Occurrence. Warwickshire, Staffordshire, Shropshire, Worcestershire and Lincolnshire.

Attachment of Scolex. When drawing up a previously published account (8) of the anatomy of this tapeworm, it was found impossible to obtain sections of the scolex *in situ* in the intestine and a description of its attachment had therefore to be omitted. Since then by great good fortune a series of sections was cut which showed this in detail. More incomplete and imperfect series confirmed the results obtained.

Upon the death of the fowl, the scolex quickly releases its hold upon the intestine. In order to see its attachment to the best advantage, it is necessary to remove the alimentary canal of the fowl as soon as possible after death, allowing an interval of twenty minutes at most to elapse. The duodenum should then be opened quickly and, if the Cestode be present, a portion cut off and placed at once without previous washing in the fixative. If however the fowl be allowed to remain unopened for half an hour, or the intestine remain opened for five minutes, the worms will be found entirely to have released their hold and be lying freely in the lumen of the duodenum. Dipping the alimentary canal in water or salt solution also causes a complete relaxation.

The scolex (Pl. XXI, fig. 25) penetrates the usual distance into the wall of the duodenum, i.e. nearly to the submucosa. In this species the suckers play a more prominent part than in most. They are cup-shaped when in use and are all four attached to the intestinal epithelium. By their own pull and the weight of the body, the tissue inside them is dragged out into small tongues, projecting from the villus into their cavities, and forming small pegs upon which they apparently hang. Being unarmed, the result is a continuous pulling strain upon the epithelium, not a breaking and disintegrating strain as in *Davainea dubius*. The damage thus done by them is consequently less, although the constant strain causes the tongues of tissue to break off from time to time. The suckers appear to bear the chief burden of fixation, and, their hold relaxing under abnormal conditions and not being more or less permanently fixed by hooks, the worm readily becomes detached from the duodenal wall.

The rostellum, unless the worm be detached from the duodenal wall, is nearly always extruded. In this condition, the knob forming its apex is considerably less in diameter than the space between the two villi. The apex of the rostellum therefore lies against one or more villi,

its hooks being firmly fixed in the tissue and its extreme apex being buried in the villus. There is thus a certain strain upon the epithelium, but in the majority of cases this does not amount to much and does comparatively little damage. It is peculiar that while sections show the hooks to be buried their whole length in tissue and the rostellum thus apparently inextricably bound to the villus, yet an exposure of five minutes to the air, or a short dip in water or salt solution, produces its complete freedom.

The whole strobila in its natural state appears to shelter as much as possible among the villi, possibly with the object of avoiding as far as possible being swept away with the food.

In some respects *Amoebotaenia sphenoides* occupies an intermediate position between *Davainea cesticillus* and *D. dubius*. In the former, attachment depends entirely upon the rostellum, the suckers taking no part: in the latter, the suckers take a prominent part, the rostellum appearing to have comparatively little function. In *Amoebotaenia sphenoides* on the other hand, the rostellum still retains its function of fixation, being aided by the powerful development of the suckers. It is possible that the powerful acetabular armature of hooks in *D. dubius* explains the paramount importance of the suckers of that species.

The behaviour of the rostellum differs in the two species of *Davainea* and in *Amoebotaenia*. In *D. cesticillus* and in the few cases of *D. dubius* where the rostellum is functional, its hooks are always inserted into the intestinal tissue, and the rostellum then retracted as far as possible into the head. In *Amoebotaenia* on the other hand, the hooks are far more deeply inserted, but the rostellum is fully extended longitudinally and contracted transversely as much as possible, the proper insertion of the hooks apparently depending upon the drag caused by the weight of the body and the action of the suckers.

From the point of view of damage to the intestine, *Amoebotaenia*, owing to its smaller size and less powerful armament, is less dangerous than either of the two species of *Davainea* above-mentioned. The damage done is comparatively slight and is confined to a small amount of fragmentation of the duodenal tissue and an unavoidable loss of blood. It is only when present in extremely large quantities that this species would be able to cause much injury to the health of its host.

Life-History. Since publishing the account of the anatomy of this species I have been able to obtain abundant material and consequently have been enabled to carry on infection experiments with a hypothetical intermediate host, the brandling (*Allolobophora foetida* Eis.). The

results were rather contradictory (Table II). Altogether 131 brandlings were fed with the ripe proglottides and of these 122 lived long enough

TABLE II.

Culture	Number of brandlings	Dates												Number infected	Number uninfected
		29. 9. 14	2. 11. 14	24. 11. 14	12. 3. 15	15. 4. 15	12. 5. 15	13. 5. 15	7. 6. 15	12. 6. 15	30. 9. 15	21. 10. 15	28. 10. 15		
1 A	10 young	S	—	E	—	—	—	—	—	—	—	—	—	3	7
2 A	10 „	S	E	—	—	—	—	—	—	—	—	—	—	3	6
3 A	10 „	S	—	E	—	—	—	—	—	—	—	—	—	2	8
4 A	10 „	S	—	E	—	—	—	—	—	—	—	—	—	4	5
5 A	10 „	S	—	E	—	—	—	—	—	—	—	—	—	2	8
6 A	10 „	S	—	E	—	—	—	—	—	—	—	—	—	1	9
7 A	10 „	S	—	E	—	—	—	—	—	—	—	—	—	7	2
1 C	10 adult	S	—	—	E	—	—	—	—	—	—	—	—	0	10
11 A	{ 5 „ } { 1 young }	—	—	—	—	S	—	E	—	—	—	—	—	0	5
12 A	10 adult	—	—	—	—	—	S	—	E	—	—	—	—	0	10
13 A	10 „	—	—	—	—	—	S	—	—	E	—	—	—	0	10
14 A	4 „	—	—	—	—	—	—	—	—	—	S	—	E	0	4
15 A	10 „	—	—	—	—	—	—	—	—	—	—	S	E	0	6
17 A	6 „	—	—	—	—	—	—	—	—	—	—	S	—	E	0
18 A	5 „	—	—	—	—	—	—	—	—	—	—	S	—	E	0
131														22	100

S=date when started. E=date when ended.

to be recorded. The low mortality is due to the easiness with which these worms can be kept in captivity. Beyond a little wet sand or blotting paper they require no food and no attention, and with only this can live for over nine months. The best place to keep them was found to be in small covered dishes or Petri dishes lined with moist blotting paper. Upon this the tapeworm proglottides were placed, fresh from the fowls' intestines and with no previous washing. Another layer of moist blotting paper was then placed over them and the worms placed in the dish. Between the two layers the worms collected and were thus constantly rubbing over the onchospheres, some of which could hardly fail to be swallowed. The first, and only successful experiments were made in this way and the brandlings kept without food all the time. It was found though that the onchospheres reached only a certain stage of development and then disappeared. This might have been due either to insufficient food or to the youth of the worms. Fresh experiments were consequently made with adult and young brandlings,

with food and without; lemco of varying percentages and decayed vegetable matter being the food used. Every case gave a negative result and not a single living egg could be found. This result entirely contradicted the previous one.

The brandlings used were of two distinct kinds, one having equal transverse bands of red and yellow, the other having the yellow bands only visible when the worm was stretched. The Rev. H. Friend, whom I questioned on the subject, was of the opinion that variations were due to differences in nutrition, but at the same time agreed that these variations might be sufficient to prevent both kinds of brandling being liable to infection by the cysticeroids.

The experiments were continued over a period of fourteen months and were thoroughly exhaustive. On the other hand, in the controls to the first series of experiments containing as many worms as the infection experiments, there were no infections at all so that the cysticeroids must have developed from the tapeworm eggs provided. Grassi and Rovelli (4) found in the brandling cysticeroids which they asserted to be those of *Amoebotaenia sphenoides*, basing their opinion upon comparisons of the hooks. This certainly confirms the first experimental results and shows that the eggs may develop inside the brandling. The hooks as figured by these investigators are rather open to suspicion however and they made no infection experiments to confirm this assertion. Also careful search in fields where infected poultry lived failed to reveal the presence of many brandlings, very often not one was found, and to account for the heavy infection they should have been present in large numbers. It seems likely therefore that in addition to the brandling some allied species of earthworm is the intermediate host.

In parenthesis a curious case of poisoning may here be recorded. On dissecting a fowl it was found to be so heavily infected that many more than the usual quantity of proglottides could be placed with the worms. Altogether four cultures were set up, three containing 10 brandlings and 50 whole strobilae each, the fourth having only 6 brandlings and 15 strobilae. Three days later when the cultures were examined it was found that in the first three experiments the majority of the worms were dead and much decayed, showing that they must have been dead at least a day: the fourth culture was all right. The survivors were removed, washed in water, and placed in fresh dishes and clean blotting paper: three days later they were dead. On the other hand, the worms from the fourth culture were entirely healthy when they were killed.

In making infection experiments with Entomotraca the same result was observed (7). The presence of many tapeworms caused a heavy mortality amongst them, and even a few worms had an appreciable effect. The explanation seems to be as there stated, that the Cestodes secrete a toxin which, when present in large quantities, acts as a strong poison, but which may have no apparent effect when diluted.

The onchosphere when swallowed by the brandling is a roughly spherical body 0.03 mm. in diameter (Pl. XIX, fig. 6). Without any apparent internal change it increases in size to 0.053×0.048 mm. and about that stage is liable to lose the embryonic hooks (Pl. XX, figs. 14, 15). Sections of this stage show it to consist of a mass of cells of two distinct sizes surrounded by an exceedingly thick membrane (Pl. XIX, fig. 7, *m.*). Several internal cavities next appear and grow until they coalesce (Pl. XX, fig. 17), occupying the whole centre of the cysticercoid, the cysticercoid being a mere hollow shell of tissue, still surrounded by a membrane but one not nearly so thick as before. Sections show the membrane to be structureless. Inside it is a thin layer of parenchyma with large nuclei disposed in a circle along its inner limit. A slight thickening can be observed at one pole. This was the highest point of development reached in the experiments.

At an early stage, while still provided with its embryonic hooks, the onchosphere penetrates the intestinal wall of its host and comes to rest in the large hepatic cells of the typhlosole. As it grows in size it necessarily distorts the intestine and causes internal change generally. The worms figured in Pl. XX, figs. 18, 19 were exceedingly heavily infected, having about 20 cysticercoids in an inch of the intestine. The intestine becomes distorted, the cavity (*i.*) almost obliterated. There is no trace of typhlosole and no distinction between the two cellular layers. Dorsal and ventral blood-vessels, if present at all, are usually too minute to be seen. The nerve-chord is pushed against the ventral body-wall. There are numerous corpuscles in the coelome but not as many as usual. A curious feature is that the cysticercoids lie loose in the intestinal wall of the host and are not attached to it. In dissecting the earthworm a prick of a needle in the exposed intestine was usually sufficient to liberate 10 to 30 cysticercoids.

Choanotaenia parina Duj.

The specimens of *Choanotaenia parina* Duj. were obtained from a number of sparrows. They varied in length from 55–66 mm. (Clerc, 50 mm.), their greatest width was 1.15–1.3 mm. (Clerc, 0.8 mm.). The

scolex was 0.17 mm. long \times 0.14–0.22 mm. wide (Clerc, 0.2 mm.). The rostellum measured in length 0.185 mm., in width 0.085 mm., and the suckers were 0.075 mm. in diameter.

The excretory system consists of the usual four longitudinal vessels with their transverse commissures. In the scolex they are connected by two circular commissures, one encircling the posterior end of the rostellum, the other its anterior end. Between these commissures run several connecting vessels.

The genital organs correspond to the usual type. The irregularly alternating genital pore lies at the anterior quarter of the segment, a little dorsal of the extreme lateral border. The cirrus-sac extends just past the longitudinal excretory vessels and has an unusually distinct inner layer of nucleated cells. It contains a straight slender cirrus, thickly studded with small spines, and at its inner end a few coils of the vas deferens. As usual the vas deferens outside the cirrus-sac coils excessively before proceeding posteriorly to the testes. These latter lie posterior to the ovary and posterior and slightly on each side of the yolk-gland. They form an irregular double layer midway between the dorsal and ventral surfaces of the proglottis.

The vagina has a small lumen and thick walls: the gland cells surrounding it are unusually large and distinct. The receptaculum seminis is spherical, situated midway between the dorsal and ventral surfaces, and in the anterior fourth of the proglottis. It communicates with the vagina by an exceedingly narrow passage.

Hymenolepis interruptus Clerc. (Plate XX.)

In dissecting a number of sparrows (*Passer domesticus* Linn.), I found in some large tapeworms belonging to the species *Hymenolepis interruptus* Clerc (2). The type species was collected from *Muscicapa atricapilla*, so that I believe this to be the first record of its occurrence from the sparrow. The worms are 35–40 mm. long (Clerc, 30 mm.) and 0.57 mm. wide (Clerc, 0.5 mm.). The scolex (Clerc, 0.45 mm.) measures 0.166 mm. long \times 0.18 mm. wide. The suckers (Clerc, 0.25 mm.) are 0.119 mm. long \times 0.091 mm. wide, and the rostellum (Clerc, 0.02 mm.) 0.128 mm. long \times 0.06 mm. wide. The ten rostellar hooks are arranged in a single row and are 0.0247 mm. long (Clerc, 0.02 mm.). In general shape they agree with those figured by Clerc, but detailed measurements show that they differ slightly in proportions.

There is a small neck present, equal in width to the scolex and not sharply distinguished from it, its length varying considerably according

to the degree of contraction. The proglottides are all broader than long with the possible exception of the most posterior: in some of the specimens the last two or three proglottides are quadrangular.

Musculature. The musculature of the strobila consists of an outer and an inner layer of longitudinal muscles, separated by an incomplete layer of circular ones. The outer longitudinal muscle layer consists of small fibres closely set together, the inner one of 18–20 (Clerc, 8) very much larger ones with large intervals between them. The fibres of both layers bend slightly towards the exterior in the centre of each proglottis. At the junctions of the proglottides is a sheet of numerous strong transverse muscles and weaker dorso-ventral ones. In the scolex, the longitudinal muscles are fixed to the suckers and rostellum, while some reach the apex of the head. The rostellum conforms to the *Amoebotaenia* type (8) with some exceptions. The inner axis of the rostellum is much smaller in proportion to the sheath and much more compact. The space between the two, instead of being filled chiefly with modified parenchyma, contains numerous muscles which serve to retract the inner axis of the rostellum.

Excretory System. There are the usual four longitudinal excretory vessels, one dorsal and one ventral each side of the proglottis. They bend outwards in the centre of each segment and inwards at its junction with its neighbours. The dorsal and ventral vessels of the same side communicate with each other by a slender dorso-ventral vessel at the posterior margin of each proglottis: posterior to the scolex there appears to be no communication between the two dorsal or between the two ventral vessels. With the exception of the scolex, the dorsal vessel remains the same width (0.007 mm. dia.) throughout the whole length of the strobilus, and does not disappear early in its course as in many species. The ventral vessel increases greatly in diameter as it goes posteriorly, until it is four times the diameter of the dorsal (0.028 mm.). In each proglottis the vessels give off numerous branches which run a short distance towards the margin and then appears to end blindly in the parenchyma. Posteriorly the vessels are situated one-sixth of the width of the proglottis from its margin, but more anteriorly this distance is increased to one-third. Just posterior to the scolex, each vessel (0.012 mm. dia.) runs outwards, nearly to the edge of the proglottis, the two vessels of the same side approaching closely to each other (Pl. XX, fig. 12, l.). Each then bends round to run almost exactly anterior and parallel to its former course, and just posterior to the posterior margin of the suckers. It does not reach as far inward as

before. At the nearest point to which they approach each other, the two vessels of the same side communicate by a rather wide dorso-ventral connection (*d.v.c.*). At this portion of their course, the four vessels have the same diameter, 0.004 mm. Half-way along the anterior course of the two parallel vessels a dorsal and a ventral branch (*s.*, *s.*') are given off to the posterior margins of the dorsal and ventral suckers respectively. Having reached their inner limit, the four vessels run anteriorly again, just exterior to and touching the outer sheath of the rostellum. The two vessels of the same side again communicate by a small dorso-ventral vessel (*d.'v.'c.'*), at about the posterior two-thirds of the length of the sucker. A short distance anteriorly the two vessels of the same side bend round to meet and fuse with each other. At the same time each gives off an exceedingly slender branch (*l.*') which penetrates the outer sheath of the rostellum and runs near its inner surface as far as the posterior level of the hooks. Here the four vessels open into a circular commissure (*c.c.*) running mid-way between the outer sheath of the rostellum and its muscular axis. This is the only connection between the vessels of opposite sides, throughout the whole course of the strobila. Along their whole course the four rostellar vessels give off numerous fine branches, some of which appear to proceed to the suckers: but as the diameter of the main vessel itself is only 0.002 mm., it is clearly impossible to follow the much smaller branches.

Male Organs. The genital pore is unilateral, slightly anterior to the mid-point between the anterior and posterior margins of the proglottis, and in transverse sections can be seen to be a little ventral of the mid-line. The cirrus-pouch (Pl. XX, fig. 10, *c.p.*) is small and cylindrical, reaching just past the dorsal longitudinal excretory vessel. It is 0.089 mm. long and 0.025 mm. wide: its inner end is 0.025 mm. from the margin of the proglottis. It opens into the dorsal side of the genital sinus, running from thence dorsally to the nervous and excretory vessels: its whole course is directed towards the dorsal surface. The cirrus-sac itself is straight, with the exception of its extreme outer end which has a slight ventral bend. The cirrus is short, straight, and unprovided with spines of any kind. At its inner end it opens into a large internal vesicula seminalis within the cirrus-sac, occupying the greater part of its length. The vas deferens running from this internal vesicula seminalis (*v.s.*) is cylindrical and curved, with the concavity directed ventrally: it lies on the dorsal surface of the proglottis, reaching nearly to the middle line. The testes (*t.*) (0.057 mm. dia.) are dorsal in position, one being situated in the pore half of the proglottis, the other two in

the opposite half: of these latter, one is placed anteriorly to and a little to the exterior of the other, their margins just touching. The testes on the pore side and the posterior testes on the other side are placed equidistant from and close to the middle line of the proglottis: they lie in the same transverse plane. All three testes are within the rectangle marked out by the four longitudinal excretory vessels. Owing to local contraction, the three lie at times in an almost straight line. The vas deferens, after leaving the inner end of the external vesicula seminalis, runs a short distance postero-transversely to half-way between the anterior and posterior margins of the proglottis, still keeping to the dorsal surface. Here it breaks up into three vasa efferentia which run to their respective testes. Although this arrangement is usually constant, in some cases the vasa efferentia from the two posterior testes unite before joining that from the anterior testis: or those from the two testes on the side opposite the genital pore similarly unite first. These cases are not very common however.

Female Organs. The vagina opens on the ventral side of the genital sinus close to the opening of the cirrus-sac. At first its diameter is very small, but about the transverse level of the outer end of the internal vesicula seminalis it widens to twice its former width. From the cirrus-sac it proceeds dorsally and slightly anteriorly to the receptaculum seminis. This latter is ovoid and situated rather anteriorly in the pore half of the proglottis, reaching nearly to the mid-line. It is 0.092–0.103 mm. long \times 0.057–0.069 mm. wide. The ducts from it run mostly dorso-ventrally and are confined within the space bounded by the two wings of the uterus, yolk-gland and receptaculum seminis. They conform to the usual type and need no special mention. The ovary is ventral and situated mid-way between the anterior and posterior borders of the proglottis. Laterally it extends nearly to the ventral longitudinal excretory vessels. Seen from the dorsal surface it is concave in shape with the cavity directed posteriorly and enclosing the compact and spherical yolk-gland. The shell-gland is very diffuse, being merely glandular matter surrounding the oviduct: it lies dorsal to the yolk-gland. The uterus is at first a narrow slender band dorsal to the ovary and in the same transverse plane as its anterior border. Later it develops two ventral wings which extend nearly to the posterior border of the proglottis and enclose a space containing the female genital ducts and the yolk-gland. At this point, its cavity begins to be incompletely subdivided by outgrowths from the walls: it extends laterally to the longitudinal excretory vessels. According to Clerc,

these two posterior wings persist in mature segments, but my own observations do not agree with this. In the more mature proglottides the two wings approach and coalesce, the uterus becomes sac-like and fills the whole proglottis, extending beyond the excretory canals. The cavity continues to be incompletely subdivided by numerous septa. The onchospheres (Clerc, 0.034 mm.) are 0.038 mm. by 0.029 mm., their hooks 0.019 mm. long (Clerc, 0.014 mm.).

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DESCRIPTION OF PLATES XIX—XXI.

REFERENCE LETTERS.

c. cirrus; *c.e.* circular excretory commissure; *c.p.* cirrus pouch; *cy.* cysticeroids; *d.v.e.*, *d.'v.'e.'* dorso-ventral excretory commissures; *g.e.* genital cloaca; *i.* lumen of intestine of brandling; *l.*, *l.'* longitudinal excretory vessel; *m.* membrane of cysticeroid; *o.* onchosphere; *ov.* ovary; *r.s.* receptaculum seminis; *s.s.'* acetabular excretory branches; *t.* testes; *ut.* uterus; *v.* vagina; *v.g.* vitelline gland; *v.s.* vesicula seminalis.

PLATE XIX.

Figs. 1–5. *Davainea dubius* n.sp.

Fig. 1. Strobila.

Fig. 2. Fourth proglottis.

Fig. 3. Self-fertilisation.

Fig. 4. Posterior proglottis.

Fig. 5. Hooks (*a*) from sucker, (*b*) from rostellum.

Figs. 6–9. *Amocbotania sphenoides* v. Lins.

Fig. 6. Mature onchosphere.

Figs. 7–9. Young cysticeroids.

PLATE XX.

Figs. 10–13. *Hymenolepis interruptus* Clerc.

Fig. 10. Proglottis with genital organs.

Fig. 11. Proglottis with uterus.

Fig. 12. Reconstruction of excretory system.

Fig. 13. Rostellar hooks, (*a*) after Clerc, enlarged by photography. The small size of the original figure would account for the slight discrepancy in measurements. (*b*) from the sparrow.

Figs. 14–19. *Amocbotania sphenoides* v. Lins

Figs. 14–15. Older onchospheres.

Fig. 16. Young cysticeroid.

Fig. 17. Section of Fig. 16.

Fig. 18. Infected brandling seen in optical section.

Fig. 19. Transverse section of infected brandling.

PLATE XXI.

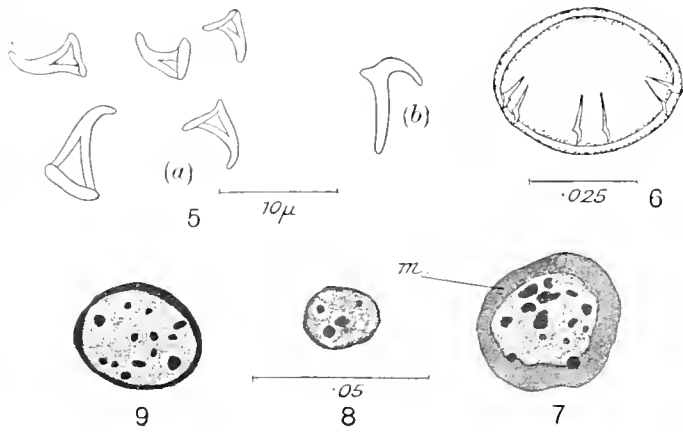
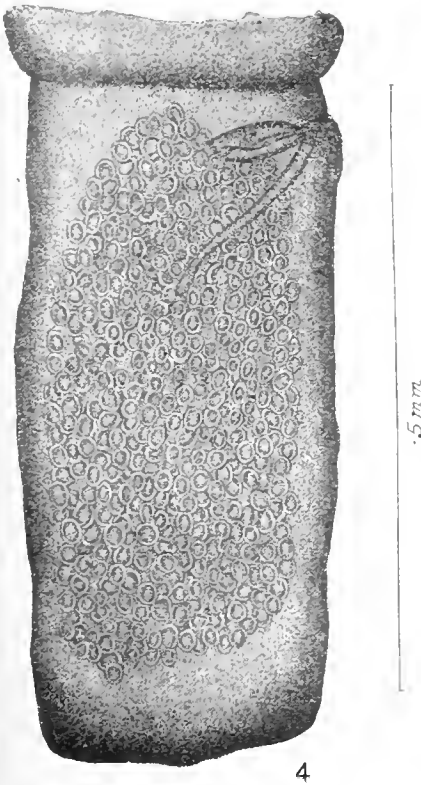
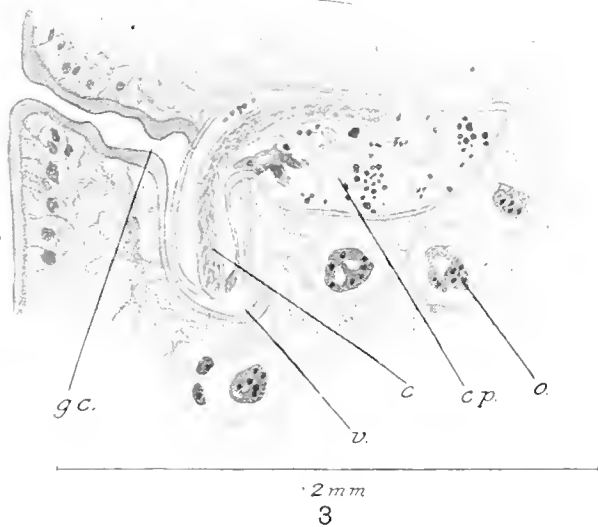
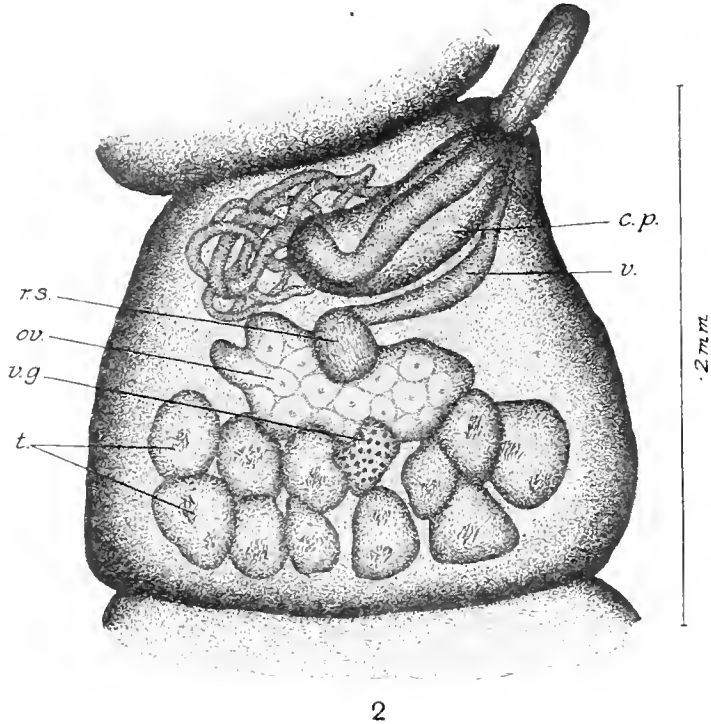
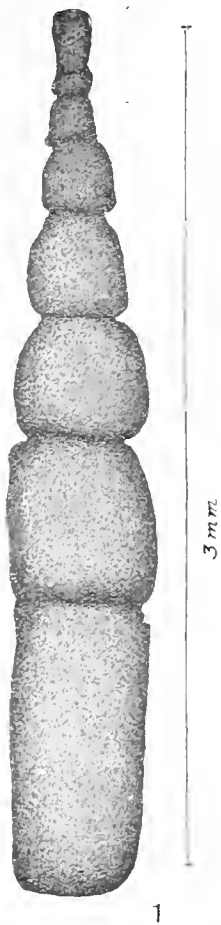
Figs. 20–22. Fowl heavily infected with tapeworms and showing emaciation. See p. 391.

Figs. 23–25. Sections of duodenum of the fowl with scolices *in situ* showing their relation to the intestinal villi.

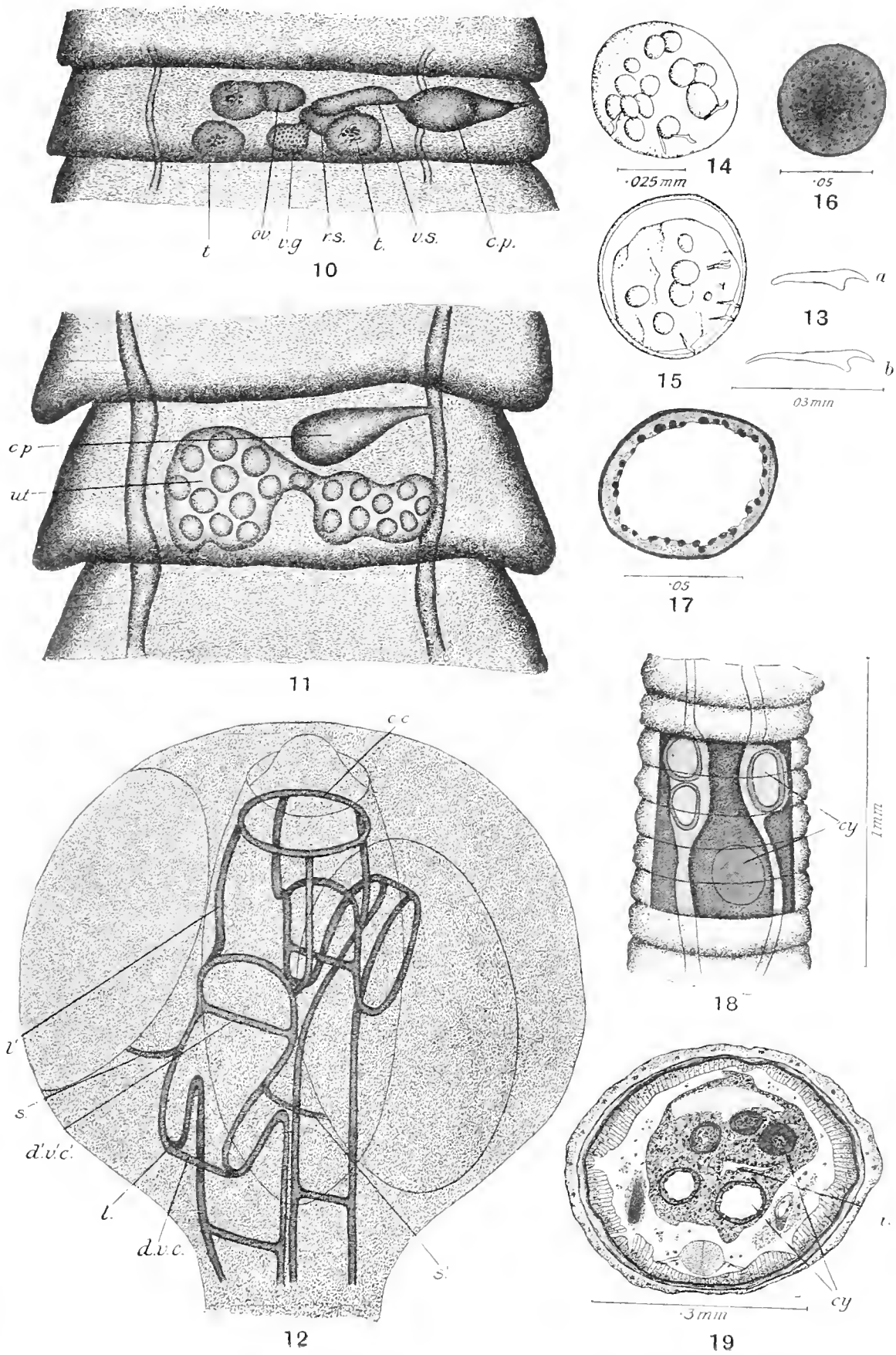
Fig. 23. Scolex of *Davainea dubius*.

Fig. 24. „ *D. cesticillus*.

Fig. 25. „ *Amocbotania sphenoides*.







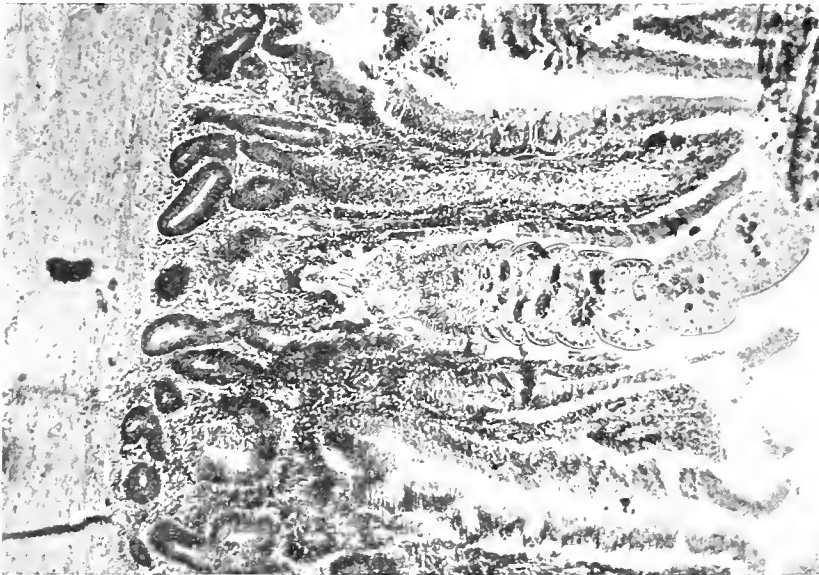




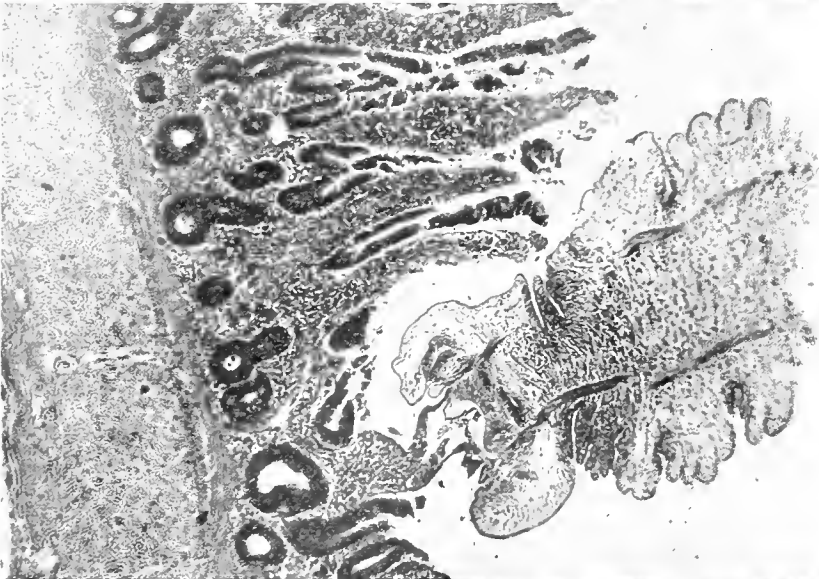


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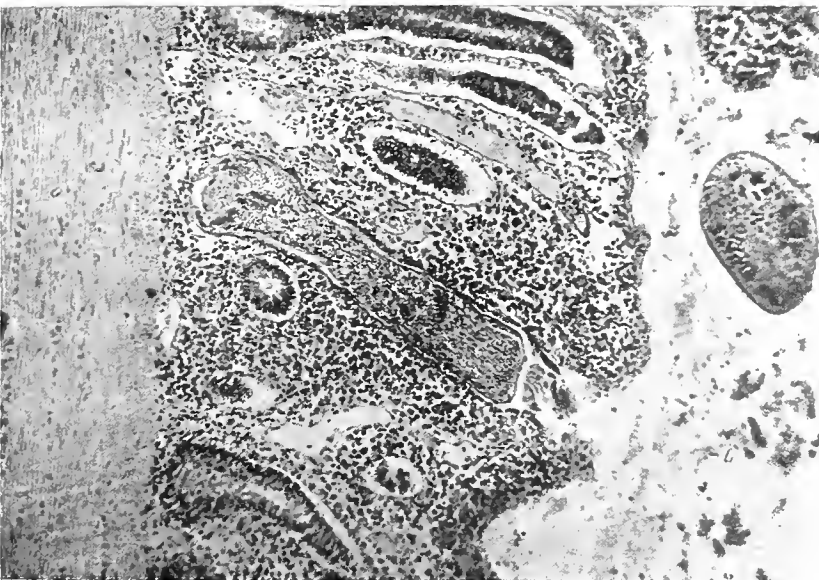




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23



THE TYPES OF THE SPECIES OF *ASCARIS* DESCRIBED BY BAIRD.

BY H. A. BAYLIS, B.A.¹

(With 3 Text-figures.)

EIGHT forms, referred to the genus *Ascaris*, were described by Dr W. Baird between 1853 and 1868, all of which are represented by type-specimens in the British Museum collection. Stossich, in his monograph of the genus *Ascaris* (1896), mentions six of them, but all these are regarded by him as *species inquirendae*. Baird's descriptions are in all cases brief, and confined almost entirely to external features, this rendering them inadequate for the requirements of present-day systematic workers. I have, therefore, thought it advisable to undertake a revision of the various types, with a view to deciding more definitely their systematic value, and, where possible, to re-describe those which appeared to me to represent valid species.

Baird's eight species are the following:

1. *Ascaris similis*, 1853. Host, a Seal (Antarctic).
2. „ *laevissima*, 1853. Host unknown (India).
3. „ *bifaria*, 1853. Host unknown (Korea).
4. „ *obconica*, 1860. Host *Helicops* [*Uranops*] *angulatus* (Brazil).
5. „ *boddaërtii*, 1860. Host *Herpetodryas boddaërtii* (West Indies).
6. „ *salvini*, 1860. Host *Oreophasis derbianus* (Guatemala).
7. „ *unduloso-striata*, 1862. Host *Sarcorhamphus papa*.
8. „ *bicolor*, 1868. Host *Odobenus rosmarus*.

Of these names, *Ascaris laevissima* and *A. bifaria* are omitted from his monograph by Stossich, who probably considered their validity too doubtful.

I have already, in a previous paper², attempted to deal with *Ascaris similis* and *A. bicolor*, upholding both these forms as valid species;

¹ Published by permission of the Trustees of the British Museum.

² *Parasitology*, Vol. VIII, No. 3, p. 360.

the specific name of the former was retained, while that of the latter was shown to have been pre-occupied, and the new name *rosmari* was suggested to replace it.

The remainder of the types have now been studied, as far as the material permits, and the following notes are intended to show the conclusions reached. *Ascaris laevissima*, *A. bifaria* and *A. unduloso-striata* seem to be incapable of support as valid species, and these specific names should, in my opinion, lapse for reasons which will be stated below. *Ascaris obconica* appears to be valid, and it has been possible to give a tolerably complete account of its anatomy. *Ascaris boddaërtii* probably represents a valid species, but on grounds of anatomy it must be removed from the genus *Ascaris*, *sensu stricto*, and placed under the category of *Polydelphis*, Dujardin. With regard to the remaining form, *Ascaris salvini*, judgment must be suspended, the sole specimen being in too poor a state to admit of anatomical investigation.

Ascaris laevissima.

Ascaris laevissima Baird, 1853 *a*, p. 25, 1853 *b*, p. 19; Pl. XXX (Annulosa), Figs. 1, 1 *a*¹.

„ „ Diesing, 1861, p. 661.

„ „ Örley, 1882, p. 310.

Of this form there is only a single specimen (female) and it is therefore impossible to examine it in detail. A study of the general external appearance, however, and especially of the shape, size and arrangement of the lips, leads me to believe that it is simply an example of *Ascaris megalcephala*² (the common Ascarid of the horse) with specimens of which I have compared it. The host and origin of the specimen are unknown. The “red circular lines at irregular distances” mentioned by Baird appear to be “scars” in the cuticle, and are probably of the nature of artifacts. The “tubercles,” or rudiments of interlabia, between the bases of the lips are a feature of *A. megalcephala*. The fine transverse striations of the cuticle, not mentioned by Baird, seem also to agree well with that species.

The transverse diameter of the dorsal lip was found to be precisely the same (1.5 mm.) as in a female *A. megalcephala*.

¹ Baird's second description of this form is a repetition of his original diagnosis, with some transpositions and slight verbal changes. Örley apparently accepts the species, but gives no description.

² Diesing (1861, p. 662) says of this and the following form: “*licet corporis proportionibus ab Ascaride megalcephala differant, tamen forma labiorum ita ad eam accedunt, ut haec tres species facile subdivisionem generis Ascaridis propriam constituere videantur.*”

Ascaris bifaria.

Ascaris bifaria Baird, 1853 *a*, p. 26; Pl. I, Figs. 2, 2 *a*. 1853 *b*, p. 19¹.

„ Dicsing, 1861, p. 661.

„ Örley, 1882, p. 310.

Of this form, as in the preceding case, there is a single specimen, which is a female, and in somewhat poor condition. It has not been possible, therefore, to do more than examine its external features. This examination, and a comparison with specimens in a better state of preservation, leads me to the conclusion that it is referable to the common *Ascaris lumbricoides* of man². This is especially borne out by the shape and size of the lips, and by the fine striations of the cuticle.

The transverse measurement of the dorsal lip (about 0.6 mm.) agrees well with that found in the female specimens of *A. lumbricoides* used for comparison.

Ascaris obconica.

Ascaris obconica Baird, 1860, p. 447.

„ „ 1861, p. 229.

„ Örley, 1882, p. 310.

„ Stossich, 1896, p. 80.

The material is contained in a bottle³ bearing the label "*Ascaris obconica* Baird. From the intestines of the *Uranops angulatus*, a fresh water snake (Brazil)." There are two male examples, and one female, in a tolerably good state of preservation. Baird's original diagnosis is very brief, and reads as follows:

"Ascaris obconica.

"Head naked; valves of the mouth small but projecting. Body of male slender for three-fourths of its length, then rapidly becoming thicker till within a line or two of the extremity, which is blunt, straight, or only slightly inflexed, and terminating in a little papilla. The skin is strongly striated. Male spicula within half a line of posterior extremity. Colour of body slightly yellow, or light straw.

"Length (male, largest specimen) 2 inches."

A re-examination of the material permits of a somewhat fuller description. The spindle-shaped thickening near the posterior end of

¹ As in the case of "*A. laevissima*," Baird's second description is a repetition of his original diagnosis, with slight changes in order and wording. Örley includes the name in his list of species, without description or comment.

² See footnote to preceding form.

³ Some smaller specimens in the same bottle prove to belong to a species of *Tanqua*.

the body is marked in both sexes, but especially in the female, and is due to the fact that the genital organs are confined to this region of the body, neither the testis nor the ovaries and uterus extending beyond the posterior third.

The largest specimen measures almost exactly 2 inches in length, as stated by Baird (52 mm. according to my measurement). This, however, is the female specimen, the males being somewhat smaller. The maximum thickness (occurring at a point about 10 mm. from the posterior end) is 2 mm.

The cuticle is thrown into marked transverse wrinkles at somewhat irregular intervals. There are also very fine and regular transverse striations, $4.2\ \mu$ apart.

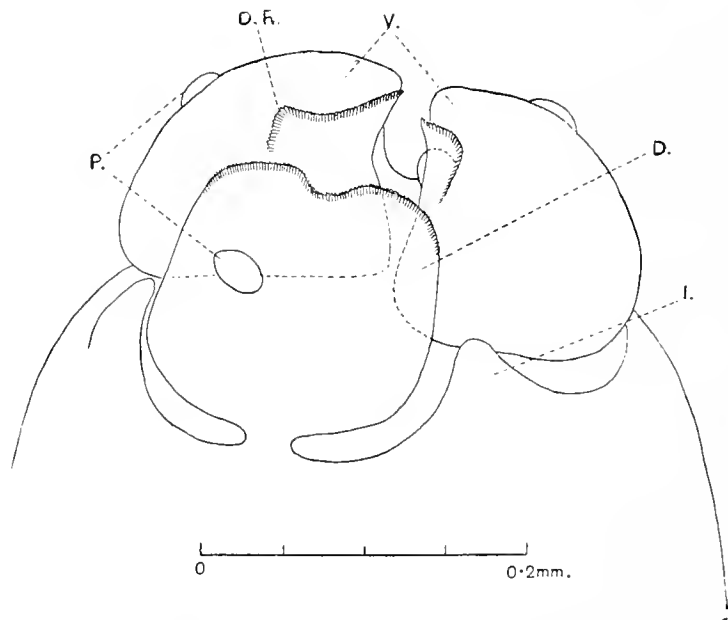


Fig. 1. *Ascaris obconica*: Nearly dorsal view of the head: *D.*, dorsal lip; *D.R.*, dentigerous ridge; *I.*, interlabium; *P.*, papillae; *V.*, ventro-lateral lips.

The lips, as seen in a lateral view (Fig. 1), are almost square in shape, with a slight indentation in the middle of the anterior margin. The dorsal lip, which is slightly smaller than the ventro-lateral lips, measures 0.17 mm. in width, and about the same in depth. There is a single large papilla on the outer surface of each lip, rather far forward. These papillae are not very prominent. The inner surface of each lip is provided with a single dentigerous ridge, with exceedingly small teeth. There are three small conical interlabia.

The oesophagus is 2-3 mm. long; it increases gradually in diameter as it passes backwards, and has a rounded base. The anterior end of the chyle-intestine is pushed forward slightly round the base of the oesophagus, forming a cup-shaped hollow into which it fits.

There are no intestinal or oesophageal diverticula.

The tail, in both sexes, is very blunt. I am unable to find the terminal papilla mentioned by Baird. In the male, the posterior end of the body has only a slight ventral flexure; the "tail," properly so-called, *i.e.* the portion posterior to the anus, measures only 0.2 mm. in length, and is curved towards the dorsal side. The spicules (Fig. 2, *Sp.*) are sickle-shaped, and have a distinct blade on the concave side.

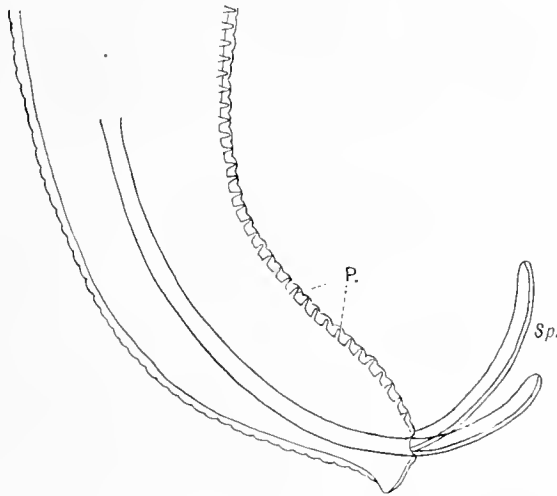


Fig. 2. *Ascaris obconica*: Lateral view of the tail in the male: *P.*, preanal papillae; *Sp.*, spicules. The postanal papillae are not shown, and the preanal papillae extend further forward than is indicated by the figure.

The back of the spicule is strengthened by a solid rib. The length of each spicule (measured in a straight line from base to tip) is 2.48 mm., and its width (including the blade) 0.08 mm. The blade is a little more than twice the width of the solid rib. There are four pairs of postanal papillae (Fig. 3, 1-4), situated close together near the extreme tip of the tail. The first pair, nearest to the tip, are rather small, and directed dorsally; the second pair larger, more bluntly conical, and more ventrally situated; the third and fourth pairs are also ventral, the fourth being about equal to the first in size, and the third intermediate between the first and second. There is a perfectly regular row of about 40 long preanal papillae on either side (Fig. 2, *P.*), the rows gradually diverging as they pass forward.

In the female, the anus is almost terminal, and the tail is bluntly rounded. The vulva is situated at 15 mm. from the posterior end. The vagina runs at first in a forward direction from the vulva, and passes, without any definite demarcation, into the uterus. At a distance of about 3 mm. in front of the vulva, the uterus bends back upon

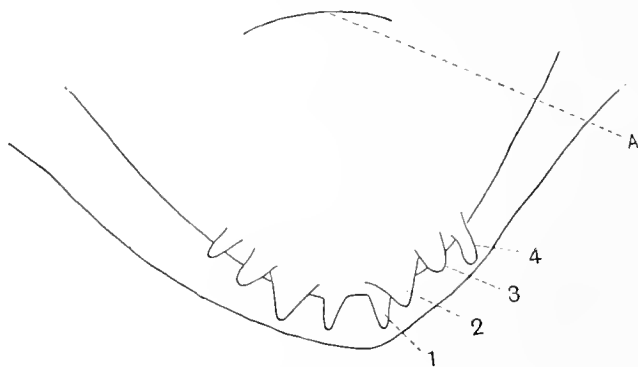


Fig. 3. *Ascaris obconica*: Ventral view (semi-diagrammatic) of the tip of the tail in the male: A., anus; 1-4, the four postanal papillae of the left side.

itself, and at 2 mm. (in a straight line) from the bend it divides into two thin-walled branches, which are packed with eggs, and run down the body together to within 6 mm. from the posterior end. The uterus and its horns, from the bend anteriorly to nearly the posterior limit, are considerably convoluted.

The eggs are spherical, and have a diameter of 100 μ . The shell is thick, and ornamented externally with somewhat coarse, rounded granulations.

The accepted name of the host from which these specimens are recorded is now *Helicops angulatus*.

Polydelphis boddaërtii.

Ascaris boddaërtii Baird, 1860, p. 447.

„ „ 1861, p. 229.

„ Örley, 1882, p. 310.

„ Stossich, 1896, p. 78.

Baird's description (1860) of this form is as follows:

“Head naked; valves of mouth distinct, large, somewhat triangular in shape. Body narrower at the anterior extremity, thicker towards the centre, and becoming narrower again at posterior extremity. Skin slightly striated; striae rather distant. Anus nearly terminal. Colour yellowish, or a deep straw-colour.

"Length of body (a female) 4 inches.

"*Hab.* Intestines of *Herpetodryas boddaërtii*, a snake from the West Indies."

Owing to the fact that there is but a single specimen, I am unable to give a complete account of the species. The following points, however, may be added to the diagnosis.

The length has been somewhat over-stated. The specimen measures 9 cm. (about $3\frac{1}{2}$ in.). The vulva is situated at 5 cm. from the anterior end. The vagina, after running in a posterior direction for about 7 mm., opens into an oval uterine chamber, measuring 3 mm. in length and 1.5 mm. in width. This gives off, laterally and posteriorly, no less than six wide uterine tubes, which follow a sinuous course, parallel to each other, backwards to within about 1.3 cm. from the posterior end of the body, where they pass into the narrower ovarian tubes. The coils of the latter occupy all the available space within the body from near the posterior end to a short distance in front of the vulva.

The presence of more than two uterine branches renders it necessary to refer this species, not to *Ascaris*, *sensu stricto*, but to *Polydelphis*, Dujardin, 1845. Whether the Ascarids of this type (*i.e.* with four or more uterine branches) should be regarded as forming a genus or a sub-genus (the latter being the view taken by Dujardin) is at present, perhaps, a matter of uncertainty. So far as is known at present, they represent a branch of the Ascarid family restricted in their habitat to the intestines of snakes.

Ascaris salvini.

Ascaris salvini Baird, 1860, p. 446.

„ „ 1861, p. 228.

„ Örley, 1882, p. 310.

„ Stossich, 1896, p. 74.

Baird's description (1860) appears to be the only one existing of this form. His second notice (1861) is a repetition, word for word, of the former diagnosis. The later authors have merely included the name of the species in their catalogues of *Ascaris*, but have added nothing to the description.

There is a single specimen, which appears to be a female, and is now in so poor a state of preservation that a fuller description is impossible. Baird, whose description is concerned only with external features, appears to have considered this form to be closely allied to *Ascaris* (*Ascaridia*) *inflexa*, and in his interleaved copy of the British

Museum Catalogue of Entozoa he has entered it in MS. as "*Ascaris* (?*Ascaridia*) *Salvini*." In view of the bad state of preservation of the specimen, it is now impossible to express an opinion as to the probability of its belonging to the genus *Ascaridia*, which would place it among the Heterakidae, as distinct from the Ascaridae.

"*Ascaris unduloso-striata*" Baird
[= *Heterakis vesicularis* (Frölich)].

Ascaris unduloso-striata Baird, 1862, p. 113.

" " Örley, 1882, p. 310.

" *noduloso-striata* Stossich, 1896, p. 73

[doubtless a misprint for *unduloso-striata*].

A bottle bearing the label "*Ascaris unduloso-striata* Baird. Ex intestinis *Sarcorhamphi papae*" contains thirteen small nematodes showing the usual characters, not of *Ascaris*, but of *Heterakis*. A careful re-examination of these specimens shows quite conclusively that they are identical with *Heterakis vesicularis* (Frölich, 1791), the type-species of the genus. This species, as is well known, is common in Gallinaeous birds, including the domestic fowl, common pheasant and partridge. It has also been recorded occasionally in ducks. It inhabits the large intestine, and more especially the caeca, of its hosts. Its presence in *Sarcorhamphus* may be the result of an "accidental infection."

A careful comparison of Baird's specimens from the King Vulture with examples of *H. vesicularis* from a domestic fowl shows that they agree very closely in all respects. The tail of the male has a similar preanal chitinous ring, and the papillae agree precisely in size, number and arrangement. In the female the size and shape of the eggs, the thickness of the egg-shells, and the position of the vulva correspond exactly in both cases; while in both sexes Baird's specimens conform to the undoubted *H. vesicularis* in the shape and dimensions of the oesophagus and its posterior bulb, and in the general arrangement of the internal organs. I have no hesitation, therefore, in concluding that these specimens from *Sarcorhamphus papa* belong to that species, in spite of the lack of close relationship between the hosts. There is nothing in Baird's brief description to contradict the present re-determination, and although he does not appear to have seen the preanal sucker-like ring in the male, which at once suggests *Heterakis*, there seems to be no doubt that these specimens constitute the types of his "species," the name of which must therefore lapse.

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SCLEROSTOME PARASITES OF THE HORSE IN ENGLAND.

I. THE GENERA *TRIODONTOPHORUS* AND *OESOPHAGODONTUS*.

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(With Plate XXII and 7 Text-figures.)

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INTRODUCTION.

SINCE the appearance in 1901 of Looss' important monograph on the Sclerostomes of Horses and Donkeys in Egypt a much greater interest has been shown in the presenee of these and allied Nematodes in other parts of the world, but, although nearly fifteen years have elapsed since that publication, very little addition has been made to our knowledge of this branch of helminthology.

Railliet and Henry (1902) were the first to show that the three species of *Sclerostomum*, as well as representatives of the three other genera established by Looss (*Cylichnostomum*, *Triodontophorus* and *Gyaloccephalus*), were of common occurrence in European countries and were abundantly represented in the Alfort collections. Leiper's (1910) list of species found in horses from the London area shows that the same genera occur in this country and we are indebted to the researches of Sweet (1909) and Gough (1908) for a few records of equine Sclerostomes in Australia and South Africa, respectively.

Much remains, however, to be done on this subject especially in England where the parasites of horses have not attracted the attention of helminthologists during recent years.

My interest in the subject was aroused in the spring of 1915 when the attention of the Birmingham Research Department, under Professor F. W. Gamble, F.R.S.¹, was directed to important outbreaks of Sclerostomiasis in horses in certain districts of Worcestershire. Thanks to the kindness of Mr J. A. Gold, M.R.C.V.S., of Redditch, I have been able to examine a number of infected animals and to assist in post-mortem investigations of cases which have had a fatal termination; specimens were also obtained from "knackers" in different parts of the Birmingham area and I am also indebted to Mr Brailsford of the Birmingham Health Department for some interesting material.

Sclerostomes are undoubtedly responsible for a considerable amount of damage to horses in this country; before any serious measures can be taken for the prevention and eradication of the disease it is absolutely essential that a good deal of information be obtained with regard to the distribution, frequency of occurrence and life-histories of the different forms connected with Sclerostomiasis. Such information is gradually being obtained; in view however of the large number of species met with during the course of my investigations it has been thought advisable to publish a systematic account of the different Sclerostomes observed before proceeding to any discussion of their bionomics or pathogenicity.

The present paper deals exclusively with the two genera *Triodontophorus* Looss and *Oesophagodontus* Railliet and Henry; of the former little seems known in England, whilst the latter has previously been observed in India and Burmah only.

¹ I wish to take this opportunity of expressing my thanks to Professor Gamble for suggesting this line of research and for his assistance in obtaining material from various sources.

Genus TRIODONTOPHORUS Looss 1901.

Triodontus Looss 1900, non Westwood 1845.

Triodontoporus Railliet and Henry 1902.

The genus *Triodontophorus* was established by Looss (1901) to include two very characteristic Sclerostomes met with in Egypt, in which the oral capsule contained three peculiarly arranged teeth arising from its floor and directed towards the mouth opening. Two species, *T. serratus* and *T. minor*, were obtained from horses and donkeys.

Railliet and Henry (1902) announced the discovery of the genus in France, but do not seem to have identified the species observed by them. *T. serratus* was later recorded by v. Linstow (1904) and Leiper (1910) from horses in India and England respectively.

A third species, *T. intermedius*, was described by Sweet (1909) from the horse in Victoria, Australia.

In addition to these three forms from the Equidae, a fourth species, *T. deminutus*, has been described from man in the tropics by Railliet and Henry (1905): these authors were able to show later (1909, 1912) that, in spite of certain superficial resemblances, especially in the structure of the oral capsule, to Looss' genus, this form belongs to a distinct genus, named by them *Ternidens*; it is more closely related to the Ocsophagostomeae than to the Cylicostomeae in which *Triodontophorus* is included.

The section Cylicostomeae of the sub-family Strongylinae¹ (Sclerostominae) is defined by Railliet and Henry (1912) as follows:

“Bourse caudale à côtés antérieures fendues, moyennes dédoublées, postérieures externes naissant isolément, postérieures tridigitées. Vulve proche de l'anús; utérus à branches parallèles. Parasites du tube digestif.”

Three species of *Triodontophorus* were found in horses in the Birmingham district, of which none could be assigned to either of Looss' species; one species is referred to *T. intermedius* Sweet, the two others are described as new.

The genus *Triodontophorus* can be defined as follows:

Cylicostomeae: Cuticle transversely striated. Mouth capsule large, with three radially-arranged teeth projecting forward into its cavity

¹ Railliet and Henry (1912) give the following definition of this sub-family of the Strongylidae: “Capsule buccale bien développée. Œufs en segmentation au moment de la ponte. Presque toujours embryon rhabditiforme et développement direct.”

from the oesophageal funnel. Six head-papillae. The anterior leaf-crown consists of numerous leaf-like elements springing from the internal surface of the well-developed mouth-collar; the posterior leaf-crown is represented by a ring of low septa-like projections, corresponding in number and distribution to the leaves of the anterior crown. The dorsal gutter of the oesophageal gland is well developed and terminates at the anterior border of the mouth capsule. The bursa of the male has a finely denticulated border, the median lobe is prominent. A dermal collar partly or completely surrounds the genital cone and the prebursal papillae are greatly elongated. The spicules are long and terminate in small hooks. The female opening is in the posterior region of the body.

***Triodontophorus intermedius* Sweet 1909.**

As mentioned above this species was described by Sweet in 1909 from three female specimens preserved in the Biological Museum of the University of Melbourne. The types were from Horsham, Victoria, and were labelled "Horse: stomach (and intestines?)"', probably in error, as from our knowledge of allied species it seems almost certain that they can only have been obtained from some part of the large intestine.

Whilst commenting on the fact that this species in some respects combines the characters of *T. serratus* and *T. minor*, Sweet remarks "one is tempted at first sight from some of the linear proportions to regard it as an immature form of *T. serratus*, but that is seen to be out of the question on examination of the reproductive organs, which are fully mature."

Among my material from the Redditch district of Worcestershire were a number of worms which I, also, originally took to be specimens of *T. serratus*; more careful examination of these showed that I was dealing with a species, quite distinct from that described by Looss, but agreeing very well with the Australian form, at least as far as the females were concerned. As both sexes were abundantly represented I am able to add considerably to Sweet's diagnosis.

SPECIFIC DIAGNOSIS. *Triodontophorus*: cuticle of the whole body transversely ringed in a similar manner to Looss' type species. The head is not sharply marked off from the rest of the body, its diameter is 200–260 μ . The mouth-collar is high, not depressed near the outer margin as in *T. serratus* and *T. minor*, on the contrary it appears approximately circular when seen in profile (Text-fig. 2 A). The external

leaf-crown consists of about forty-eight leaves, an equal number of small plates project from their bases into the cavity of the mouth capsule and constitute the internal leaf-crown. The mouth capsule is a little broader than high, measuring $150\text{--}180\mu$ in maximum breadth and $100\text{--}130\mu$ in length. The three large teeth have their anterior margins denticulated as in *T. serratus* (Text-fig. 2 A).

The oesophagus measures $0.97\text{--}1.3$ mm. in length. A pair of cervical papillae are situated at about the level of the excretory opening, $620\text{--}700\mu$ from the anterior extremity.

Female: $16.5\text{--}18.7$ mm. in length. The body attains a maximum thickness of $650\text{--}750\mu$ near the middle, this becomes reduced to $400\text{--}500\mu$ at the level of the base of the oesophagus. The "tail region" is elongated but not to quite the same extent as in *T. serratus*, the distance of the vulva being $1.45\text{--}1.7$ mm., that of the anus 450μ from the posterior extremity (cf. Text-fig. 3 A). The body has a diameter of about 450μ at the level of the vulva, behind this point it tapers rapidly giving the whole tail region a very pointed appearance when viewed under a low magnification (Text-fig. 1 A). The eggs are considerably smaller than those of *T. serratus* as figured by Looss¹, they measure $90\text{--}100\mu$ in length and $40\text{--}50\mu$ in breadth.

Male: $14.5\text{--}15.5$ mm. in length, about 650μ in thickness near the middle of the body and $400\text{--}450\mu$ at the base of the bursa. The bursa has an approximate width of 800μ , the median lobe is short and wide and is similar to that of *T. serratus*; as in the latter species the dermal collar of the genital cone covers its anterior face only. The prebursal papillae and the rays of the bursa also very closely resemble those of *T. serratus* (Text-fig. 4 A). As in Looss' species the spicules are very thick and provided with relatively small, strongly recurved hooks (Text-fig. 6 A); they differ from those of *T. serratus* in the possession of stout barbs projecting backwards from the shafts a short distance behind the hooks. The spicules are enclosed in a delicate, finely striated sheath.

T. intermedius was found on several occasions in company with other Sclerostomes, both in the colon and caecum. Although many specimens were collected it never occurred in sufficient numbers to be suspected of causing symptoms of Sclerostomiasis.

¹ In his monograph (1901) Looss omits the measurements of the eggs; he, however, figures those of both species of *Triodontophorus* in his memoir on *Anchylostomum duodenale* (1911), his figures are $\times 310$ which gives a length of about 130μ in *T. serratus* and 97μ in *T. minor*.

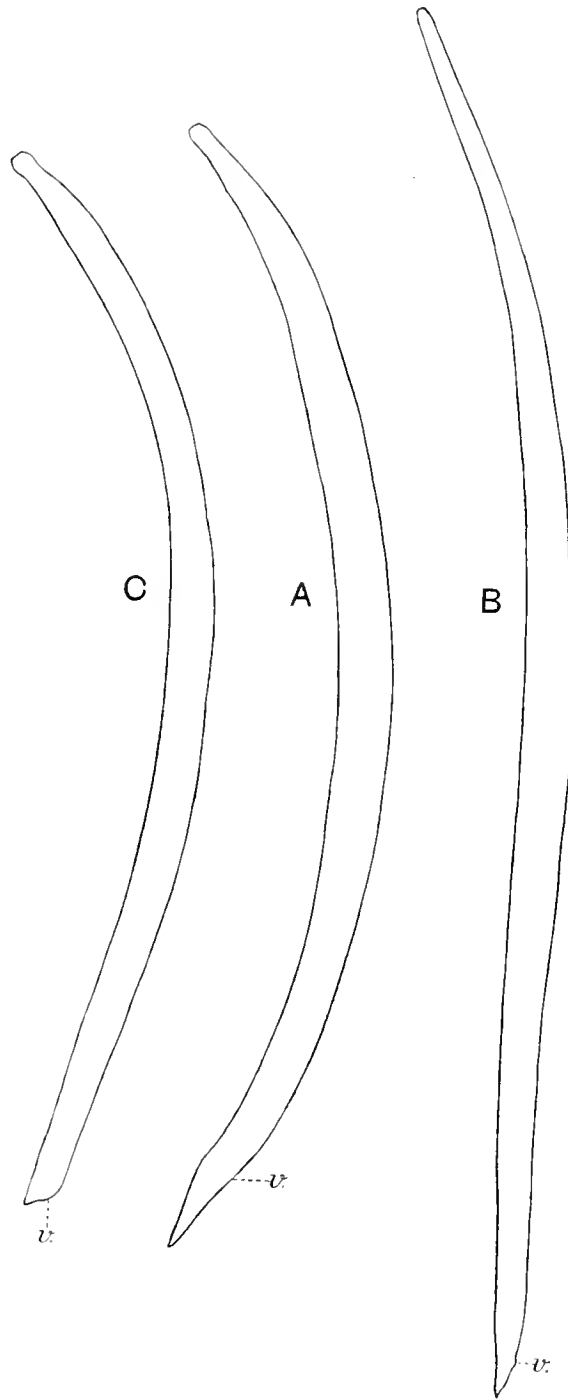


Fig. 1. Outline drawings of the females of three species of *Tridontophorus*, viewed from right side. A. *T. intermedius* Sweet. B. *T. tenuicollis* sp. n. C. *T. brevicauda* sp. n. v. shows position of vulva. $\times 8$.

T. intermedius is certainly very closely allied to *T. serratus*, it can however be readily distinguished from that species by its smaller size, the shape of the mouth-collar, the position of the vulva and the size of the eggs in the females, and by the character of the spicules in the males.

***Triodontophorus tenuicollis* sp. n.**

SPECIFIC DIAGNOSIS. *Triodontophorus*: the body attains its greatest thickness near the middle and tapers markedly towards both extremities; the thickness at the level of the base of the oesophagus is less than half the maximum thickness. The cuticle is transversely ringed, near the middle and at the posterior extremity these cuticular rings are much as in the other species of the genus, in the narrow anterior region they are, however, much accentuated and modified in such a way as to give the body-margins a coarsely serrated appearance (Text-fig. 2 B).

The head is not separated from the body and is smaller than in the other species, its diameter varies from $150\text{--}200\mu$. The mouth-collar is depressed as in *T. minor* Looss; the elements of the external and internal leaf-crowns number 40–44. Owing to the small size of the head the dimensions of the mouth capsule are also much reduced, it has a breadth of $110\text{--}140\mu$ and a maximum length of $70\text{--}90\mu$. The anterior margins of the teeth are provided with sharp denticulations as in *T. serratus* and *T. intermedius* (Text-fig. 2 B).

The oesophagus is rather short, measuring $620\text{--}900\mu$. The excretory pore is at about the same level as the cervical papillae, $680\text{--}750\mu$ from the anterior end.

Female: $16\text{--}19.5$ mm. in length. The maximum thickness near the middle of the body is $700\text{--}770\mu$, whilst opposite the termination of the oesophagus it measures only $280\text{--}300\mu$. The body also tapers considerably towards the posterior end and the thickness at the level of the vulva is considerably less than in the other species, being only $250\text{--}300\mu$. The tail region is short, the vulva being situated $460\text{--}560\mu$ from the posterior extremity. The anus is about 120μ from the end of the body (Text-fig. 3 B).

The eggs are indistinguishable from those of the preceding species.

Male: $13.5\text{--}19$ mm. in length; the greatest thickness near the middle is $450\text{--}650\mu$, at the termination of the oesophagus $230\text{--}250\mu$. The body also tapers towards the bursa, the breadth at the base of that structure being $280\text{--}350\mu$.

The bursa has about the same width as that of *T. intermedius* and is also provided with a short median lobe, the latter, however, is more

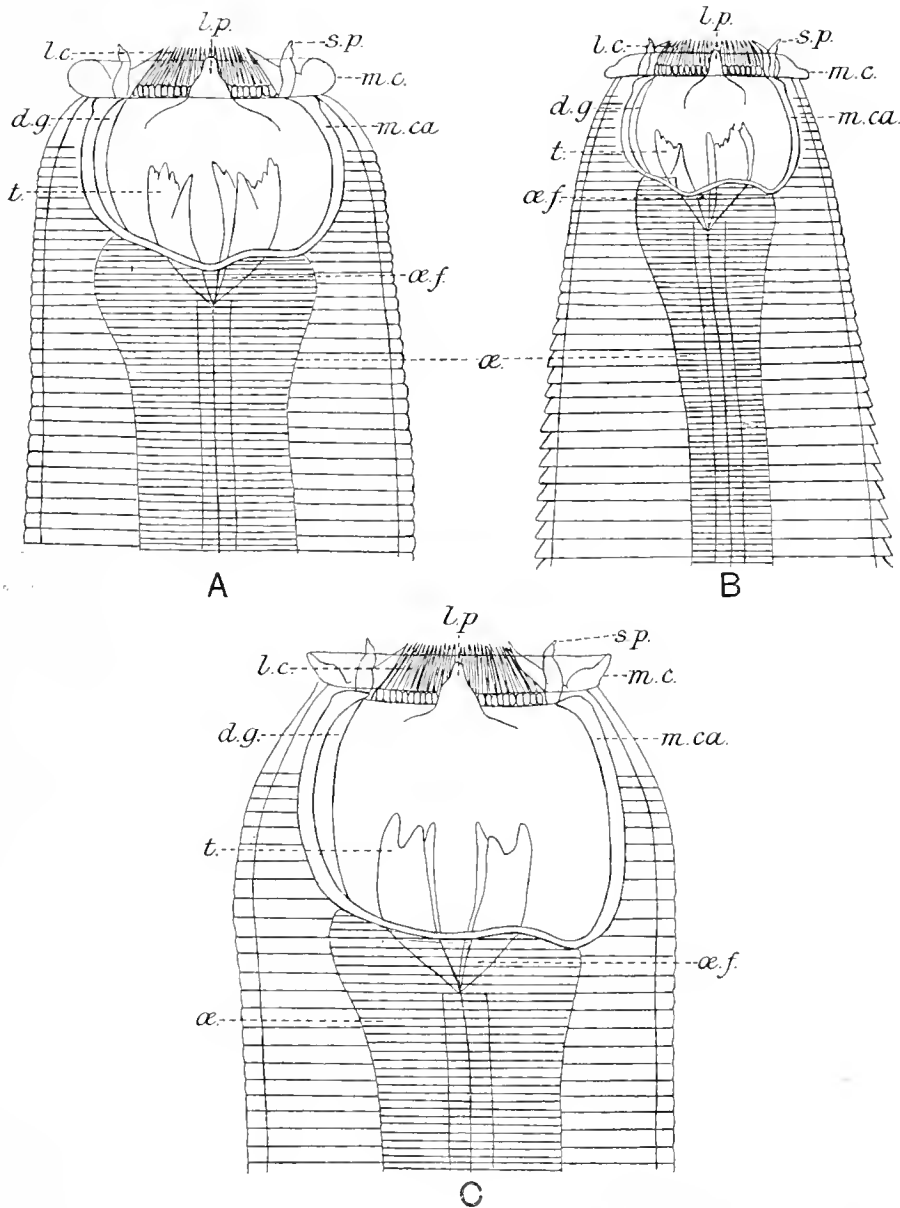


Fig. 2. Anterior extremities of the three species of *Tridontophorus*, viewed from right side. A. *T. intermedius* Sweet. B. *T. tenuicollis* sp. n. C. *T. brevicauda* sp. n. l.p. lateral head papilla. m.c. mouth-collar. m.ca. mouth capsule. oe. oesophagus. oe.f. oesophageal funnel. s.p. sub-median head-papilla. d.g. dorsal gutter of oesophageal gland. l.c. leaf-crown. t. tooth. $\times 150$.

sharply marked off from the lateral lobes (Text-fig. 5 B) and is also carried in a somewhat different manner: when seen in a side view

(Text-fig. 4 B) it appears almost at right angles to the longitudinal axis of the body. The dermal collar is enormously developed and completely surrounds the genital cone, in consequence the prebursal papillae

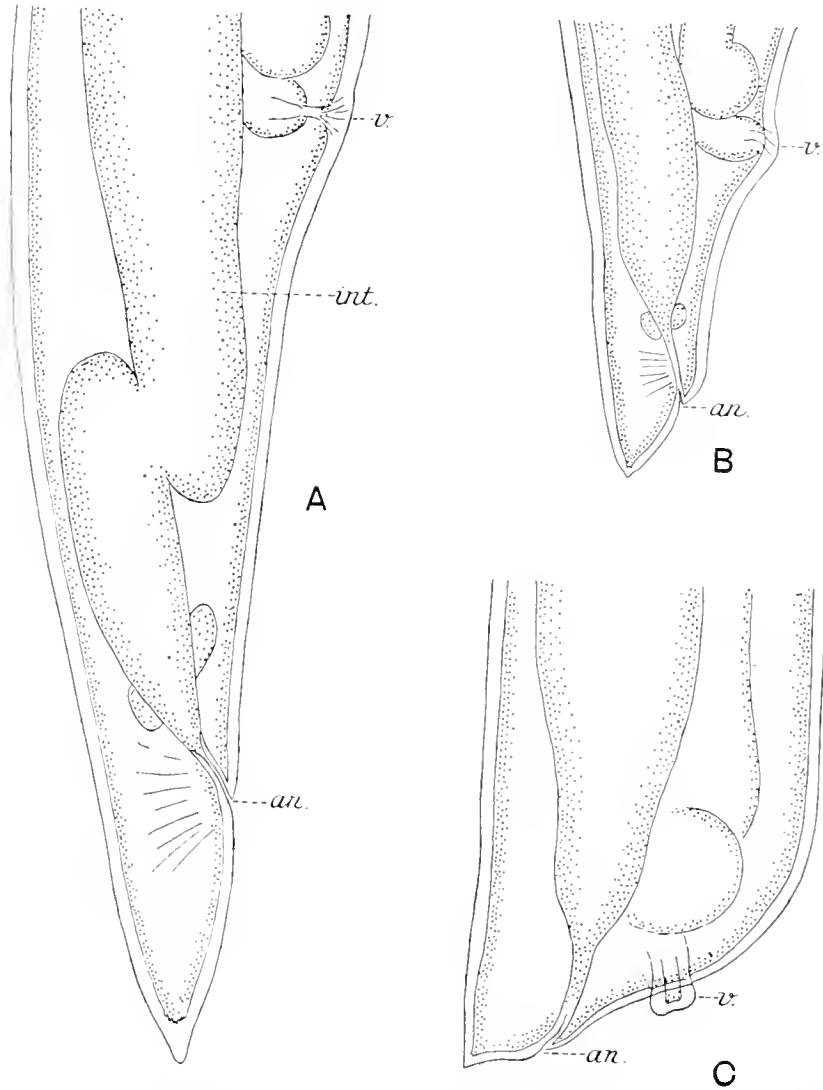


Fig. 3. Posterior extremities of females, viewed from right side. A. *T. intermedius* Sweet. B. *T. tenuicollis* sp. n. C. *T. brevicauda* sp. n. an. anus. int. intestine. v. vulva. $\times 75$.

have become greatly elongated. The rays of the bursa resemble those of *T. intermedius*, the tips of the ventral rays are however slightly more divergent.

The spicules are very slender and have characteristic terminations (Text-fig. 6 B), the hooks being feebly developed and forming wide angles with the shafts.

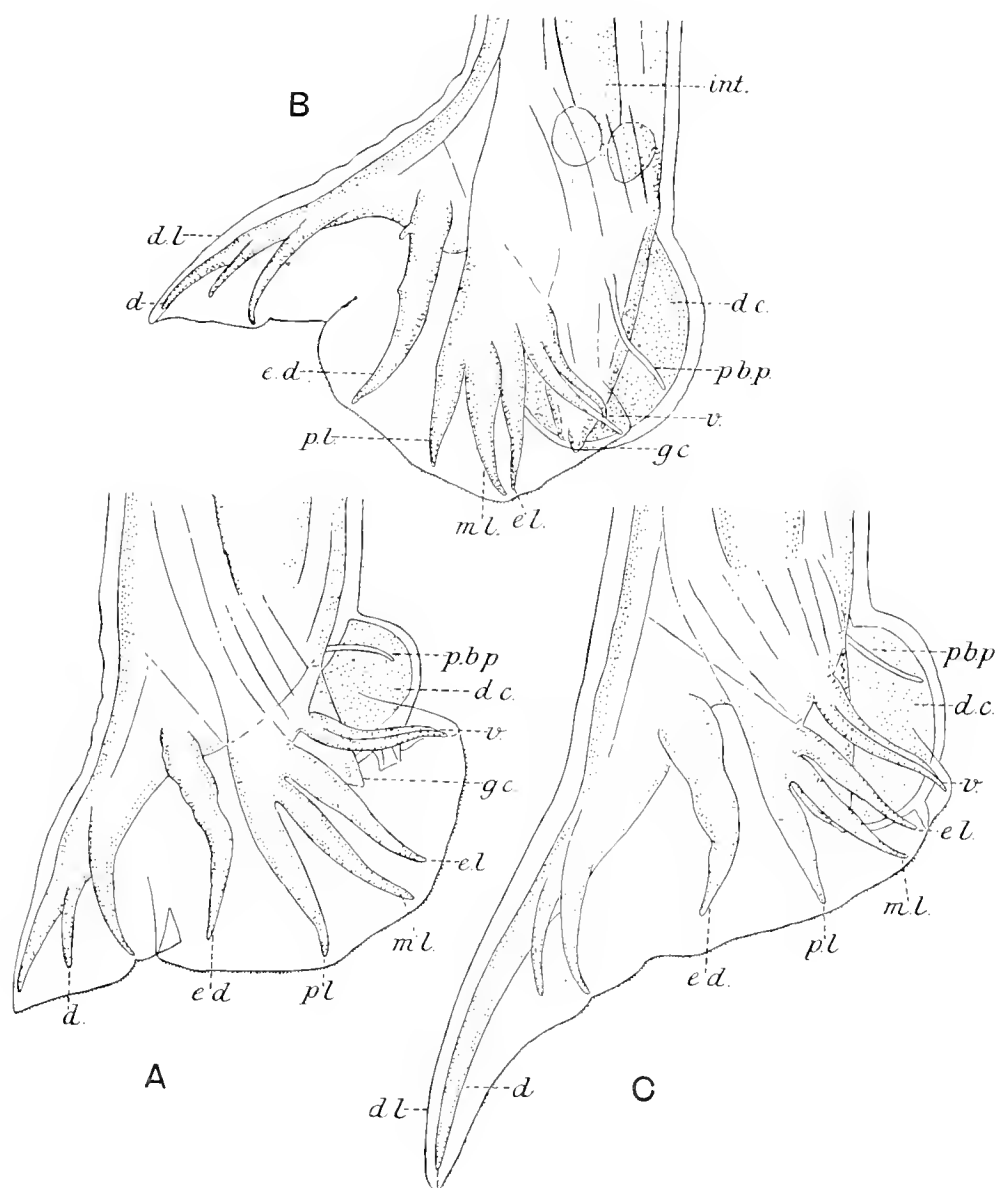


Fig. 4. Male genital bursae viewed from right side. A. *T. intermedius* Sweet. B. *T. tenuicollis* sp.n. C. *T. brevicauda* sp.n. *d.* dorsal rays. *d.c.* dermal collar of genital conc. *d.l.* dorsal lobe. *e.d.* externo-dorsal ray. *e.l.* externo-lateral ray. *g.c.* genital cone. *int.* intestine. *m.l.* medio-lateral ray. *p.b.p.* prebursal papilla. *p.l.* postero-lateral ray. *v.* ventral rays. $\times 75$.

This species is by far the most abundant of the three observed in the Birmingham district, it was found on several occasions in enormous numbers in the colon and caecum in horses suffering from intestinal and other troubles. When alive *T. tenuicollis* is semi-transparent of a whitish colour, tinged with a blood-red pigment: the latter is often restricted to the anterior end and in this position is most brilliant, the coloured extremity contrasting vividly with the rest of the body. The pigment lies partly in the body-cavity and therefore cannot be considered simply as blood derived from the host¹.

***Triodontophorus brevicauda* sp. n.**

SPECIFIC DIAGNOSIS. *Triodontophorus*: the body appears rather blunt owing to the somewhat thick extremities. The head is broad (270–325 μ) and separated from the body by a gentle constriction behind the mouth capsule. The mouth-collar is very characteristic, being high and erect, attaining its greatest breadth anteriorly so as to appear separated from the rest of the head by a deep constriction (Text-fig. 2 C). Owing to the large size of the head the elements of the leaf-crowns are more numerous than in the preceding species, the average number being 60.

The mouth capsule is large, appearing nearly as long as broad and measuring 160–210 μ by 200–250 μ . The anterior edges of the teeth are not denticulated and present a similar appearance to those of *T. minor* Looss (Text-fig. 2 C). The cuticle of the whole body is transversely ringed.

The oesophagus varies in length from 0.9 to 1.4 mm. The cervical papillae are, as in the other species, situated close to the level of the excretory pore, 730–880 μ from the anterior end.

Female: 16–17 mm. in length. The body has a thickness of 670–700 μ in the middle and tapers gently towards the anterior extremity, the thickness at the level of the oesophageal termination being about 500 μ . The shape of the posterior extremity is very characteristic; the anus is only 100–130 μ from the end and the vulva is immediately in front of it (Text-fig. 3 C), the distance between the two openings averaging 170 μ . The body has a breadth of about 420 μ just in front of the vulva and tapers so suddenly behind this point that the whole

¹ Cf. Looss' remarks on the coloration of *Anchylostoma duodenale* (1905, p. 32), also Boulenger (1915, p. 137).

tail region appears obliquely truncated when seen under a low magnification (Text-fig. 1 C).

The eggs as in the preceding species measure $90\text{--}100\mu$ in length.

Male: $13.5\text{--}14$ mm. in length. The breadth in the middle of the body is $600\text{--}650\mu$, at the base of the bursa $400\text{--}460\mu$. The bursa is characterised by the greatly elongated median lobe (Text-figs. 4 and 5 C)

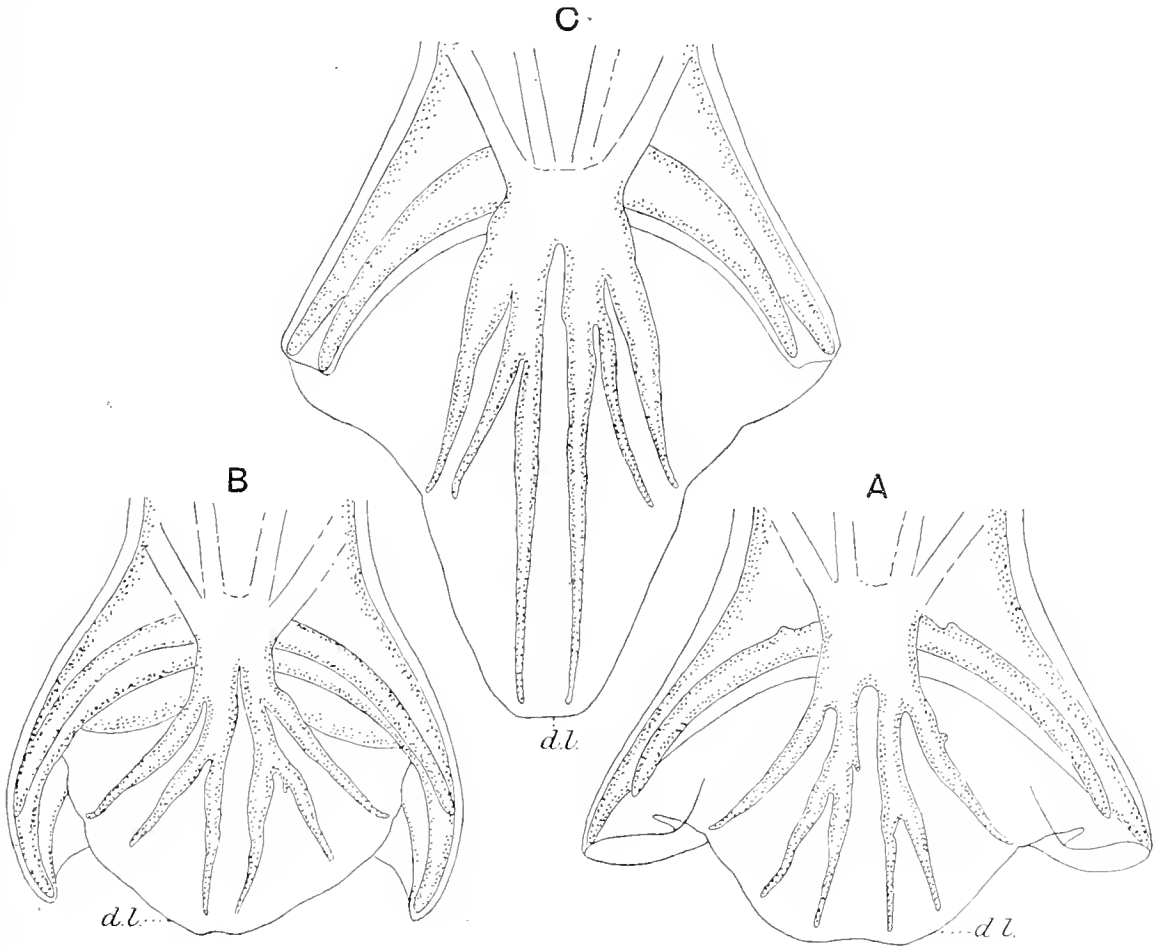


Fig. 5. Male genital bursae viewed from dorsal side. A. *T. intermedius* Sweet. B. *T. tenuicollis* sp. n. C. *T. brevicauda* sp. n. d.l. dorsal lobe with six dorsal rays. $\times 75$.

and the corresponding length of the dorsal rays which measure up to 750μ . As in *T. minor* the dermal collar completely surrounds the genital cone (Text-fig. 4 C), it is however not developed to the same extent as in *T. tenuicollis* and the prebursal papillae are consequently a little shorter than in that species.

The spicules are slender (Text-fig. 6 C), the hooks are more strongly recurved than in *T. tenuicollis* and are further characterised by the peculiar hammer-shaped "barbs" at their junctions with the shafts.

T. brevicauda was found in the colon and caecum on several occasions, like *T. intermedius* it never occurred in large numbers. The species is obviously closely allied to *T. minor* Looss; it can, however, be readily distinguished by the shape of the mouth-collar, by the peculiar structure of the tail region in the females, and by the characters of the spicules in the males.

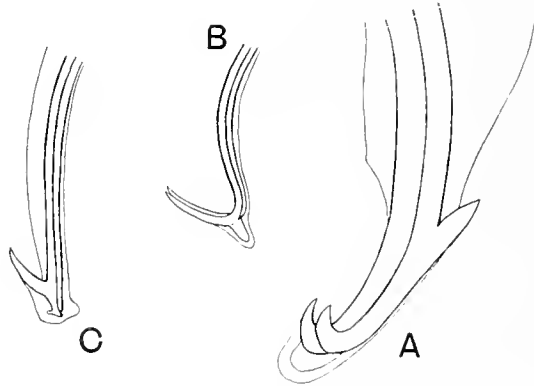


Fig. 6. Terminal portions of spicules. A. *T. intermedius* Sweet. B. *T. tenuicollis* sp. n. C. *T. brevicauda* sp. n. $\times 375$.

It will be seen from the diagnoses given above that, apart from size, the various species of *Triodontophorus* are distinguishable by the combinations of various well-marked characters, the most important of which are: in both sexes, the shape of mouth-collar and the shape and size of the oral capsule; in the females, the shape of the "tail" and the distance of the vulva from the posterior extremity; in the males, the form and size of the dorsal lobe of the bursa and the spicules. The more important of the distinctive characters are tabulated on the opposite page; in the case of *T. serratus* and *T. minor* the various measurements have been obtained from Looss' monograph (1901), either from the text or the plates.

TRIODONTOPHORUS.

	<i>T. serratus</i>	<i>T. intermedius</i>	<i>T. tenuicollis</i>	<i>T. brevicauda</i>	<i>T. minor</i>
Length of female	25 mm.	16.5-18.7 mm.	16-19.5 mm.	16-17 mm.	14 mm.
Length of male	18 mm.	14.5-15.5 mm.	13.5-19 mm.	13.5-14 mm.	13 mm.
Mouth collar ...	Slightly depressed at margin	Circular in profile	Depressed at margin	Erect	Depressed at margin
Elements of leaf-crown ...	52-55	48	40-44	60	44-49
Mouth capsule:					
Height ...	0.12 mm.	0.1-0.13 mm.	0.07-0.09 mm.	0.16-0.21 mm.	0.19 mm.
Breadth ...	0.18 mm.	0.15-0.18 mm.	0.11-0.14 mm.	0.2-0.25 mm.	0.19 mm.
Capsule teeth:					
margins ...	Denticulated	Denticulated	Denticulated	Not denticulated	Not denticulated
Vulva from post. end ...	More than 2 mm.	1.45-1.7 mm.	0.46-0.56 mm.	About 0.3 mm.	About 0.7 mm.
Dorsal lobe of bursa ...	Short	Short	Short, sharply marked off from lateral lobes	Long	Long
Dermal collar of genital cone	Covers anterior surface	Covers anterior surface	Completely surrounds cone	Completely surrounds cone	Almost completely surrounds cone
Spicules ...	Comparatively thick	Comparatively thick	Slender	Slender	Slender
„ Length	4 mm.	3.5 mm.	1.25 mm.	1.75 mm.	1.8 mm.

Genus OESOPHAGODONTUS Railliet and Henry.

Oesophagodontus robustus Giles.*Sclerostomum robustum* Giles 1892.*Oesophagodontus robustus* Railliet and Henry 1902.

This species was described under the name *Sclerostomum robustum* by Giles (1892), who observed a large number of specimens in horses and mules in India, they occurred in the colon and caecum in company with other worms and were, at least partly, responsible for the severe symptoms of sclerostomiasis exhibited by their hosts.

Although the species has not been rediscovered since that date, it has figured frequently in helminthological literature. Giles' description was published before the old-established genus *Sclerostomum* was split up by Looss (1900) and, although on most points accurate, for this reason remained incomplete as regards a number of characters now recognised as of systematic importance, the result being a considerable

divergence of opinion as to the exact position of the worm in modern classifications.

Looss (1900) was inclined to include *S. robustum* in his genus *Triodontophorus*; Railliet and Henry (1902), however, expressed the opinion that if Giles' description and figures were accurate the parasite could not be included in any of the known genera, and proposed for it the new generic name *Ocsophagodontus*. In a later paper (1912) these authors assign their genus to the sub-family CYLICOSTOMEAE, close to *Cylichnostomum*.

Material was obtained by me near Redditch in Worcestershire on one occasion only, from the colon of a mare which had died suddenly after showing symptoms of severe sclerostomiasis. About a dozen specimens were collected from among an enormous number of *Triodontophorus tenuicollis* and *Cylichnostomum* spp., examination of these showed that Giles' description of the species was on the whole correct; I have, however, been able to add to his account and my observations also show that Railliet and Henry were undoubtedly right in their estimate of the systematic position of this interesting worm.

SPECIFIC DIAGNOSIS. The body is stout, tapering only slightly towards the anterior extremity. During life the worms have a brownish colour and the intestine is deeply pigmented, showing through the semi-transparent body-wall.

The cuticle is provided with transverse ridges as in *Triodontophorus*. The head is separated from the body by a slightly constricted neck and is of considerable breadth, measuring 500–800 μ . The mouth-collar is depressed and its oral margin considerably notched so as to present a tuberculated appearance (Plate XXII, fig. 3). As in the genus *Cylichnostomum* there are anterior and posterior leaf-crowns, each composed of distinct leaf-shaped elements; the leaves of the anterior crown are large and usually number about 18, those of the posterior crown are considerably smaller, they are rather difficult to count, but, as far as I could ascertain, their usual number is about 36.

As in other Sclerostominae six head papillae are present, two lateral and four sub-median. The lateral papillae are not markedly raised from the surface of the mouth-collar, their bases are rather broad and carry a pair of lateral horn-like processes; a pair of similar but smaller processes are situated near the anterior extremity of each papilla (cf. Plate XXII, fig. 3, *L.P.*). Each sub-median papilla consists of a slender tactile appendage carried on a basal, wart-like prominence

of the mouth-collar, this basal region bears in addition a second appendage in the form of a delicate trumpet-shaped process directed externally (Plate XXII, fig. 3, *Sm.P.*).

The mouth capsule is goblet-shaped, it attains its greatest width of $0.32-0.47\mu$ near its anterior margin and narrows considerably posteriorly. Its length varies from $0.22-0.32\mu$. The wall of the capsule is comparatively thin except posteriorly where it is greatly thickened in such a manner as to form a hoop-like transverse ridge encircling the base of the mouth capsule, an exaggeration of the conditions prevailing in some of the larger species of *Cylichnostomum*, e.g. *C. elongatum* (cf. Plate XXII, fig. 3, *M.C.*). There is no dorsal gutter, the dorsal oesophageal gland opening at the base of the capsule.

The oesophagus has a length of $1.3-1.7$ mm., it is broadest anteriorly, just behind the mouth capsule, and narrows somewhat towards the middle, increasing again in width posteriorly. The oesophageal funnel is well developed and the lining of its triradiate cavity is modified to form three tooth-like structures, which do not however protrude into the mouth capsule; the general structure of the funnel can be considered as an exaggeration of that met with in some species of *Cylichnostomum*, e.g. *C. elongatum* (Looss 1901, p. 129). The excretory pore (Plate XXII, fig. 2) and the cervical papillae occupy a position slightly posterior to the nerve-collar, about 1.2 mm. from the anterior end. The cervical papillae are extremely small and difficult to see.

Females: $19-22$ mm. in length with a maximum thickness of $1.1-1.5$ mm. in the middle of the body; this thickness is maintained behind the middle until the level of the vulva which is situated $2.8-3.7$ mm. from the posterior extremity; behind this point the body tapers rapidly to the end forming a pointed tail region (Plate XXII, fig. 4). The anus lies $0.5-0.7$ mm. from the posterior end. The extremity of the tail has a rather variable shape according to the degree of contraction, it frequently appears mucronate as described by Giles.

The female genital organs are arranged on the plan common to all the CYLICOSTOMEAE, that is to say the two uteri are parallel.

The eggs are large, oval and thin-shelled, they measure $100-130\mu$ in length by $50-60\mu$ in breadth. They are laid in the early morula stage (Plate XXII, fig. 7).

Males: $15-16$ mm. in length, the body is thickest ($0.95-1$ mm.) in the middle decreasing slowly towards the bursa and measuring $0.45-0.5$ mm. in width at the base of that organ.

The bursa has a breadth of 0.9 to 1 mm., as described by Giles it is

peculiar in being bilobed, no trace of a median (dorsal) lobe being present (Text-fig. 7). The margins of the lateral lobes are finely denticulated as in the genus *Triodontophorus*. The ventral rays are slender and parallel, and of equal size. The medio-lateral ray is a little shorter than the other lateral rays and the postero-lateral is peculiar in possessing a short thick branch arising from near its base and projecting dorsally (Plate XXII, fig. 5, *A.P.l.*); this extra lateral ray terminates very bluntly, its exact shape and length vary considerably¹. There is no median dorsal ray, the dorsal rays arising in two groups of four (Text-fig. 7 and Plate XXII, fig. 5). The externo-dorsal is the longest, the three other dorsals being sub-equal, the middle one is, however, a little shorter than the others.

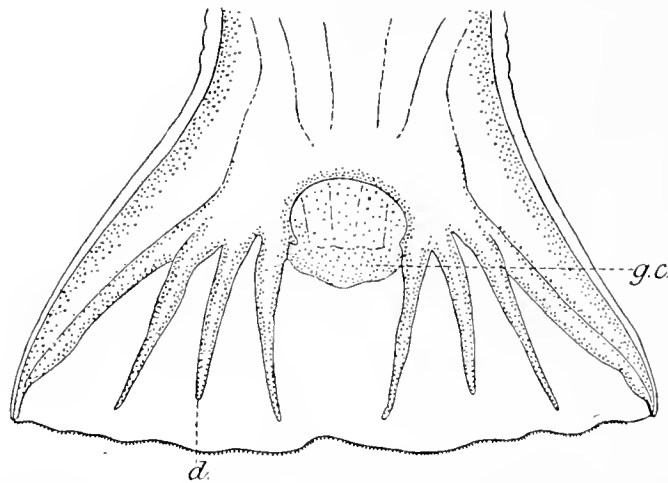


Fig. 7. Dorsal view of bursa of *Oesophagodontus robustus* Giles. *d.* dorsal rays. *g.c.* genital cone.

The genital cone (Plate XXII, fig. 6 and Text-fig. 7) is short and broad, its shape being almost hemispherical; it bears a pair of small lateral papillae, whilst a conical lip-like process is situated medianly, just ventral to the cloacal opening.

As in *Triodontophorus* and *Cylichnostomum* the dermal collar (Plate XXII, figs. 5 and 6) is well developed, it occupies the ventral aspect of the genital cone only. The prebursal papillae are short.

¹ A very similar appendix to the postero-lateral ray is met with in *Choniangium epistomum* Piana and Stazzi (= *Asifia vasifa* Lane), a sclerostome parasite of the Indian elephant. Lane (1914) evidently overlooked Giles' species when he wrote "any multiplication of the lateral rays of a bursate nematode appears to be hitherto unknown, and the presence of this feature in the form just described to be unique." Cf. also Railliet, Henry et Bauche (1914).

The spicules are long and slender, they end bluntly without hook-like terminations, they are enclosed in a finely striated sheath, very conspicuous when the spicules are protruded (Plate XXII, fig. 5, *Sp.*).

It will be seen from the above diagnosis that a serious discrepancy exists between it and Giles' account with regard to the position of the vulva; Giles gives the distance between this opening and the anus as about 1 mm. whilst in the specimens examined by me it varied between 2.3 and 3 mm. Giles, however, gives a figure of a pair of the worms *in copula* in which the position of the female genital opening is certainly further from the posterior extremity than is stated in the text. I think therefore that we may assume that his measurement was given in error.

The eggs in the specimens described by me are also a little smaller than those recorded by Giles, this author gives the egg measurements as $152 \times 82 \mu$; he does not say whether the eggs measured were taken from the maternal uterus or from the faeces of the host; those referred to in my diagnosis are all from the former source, it is a well-known fact that the eggs of various helminths swell considerably after being deposited and it is possible that the discrepancy is due to some such cause.

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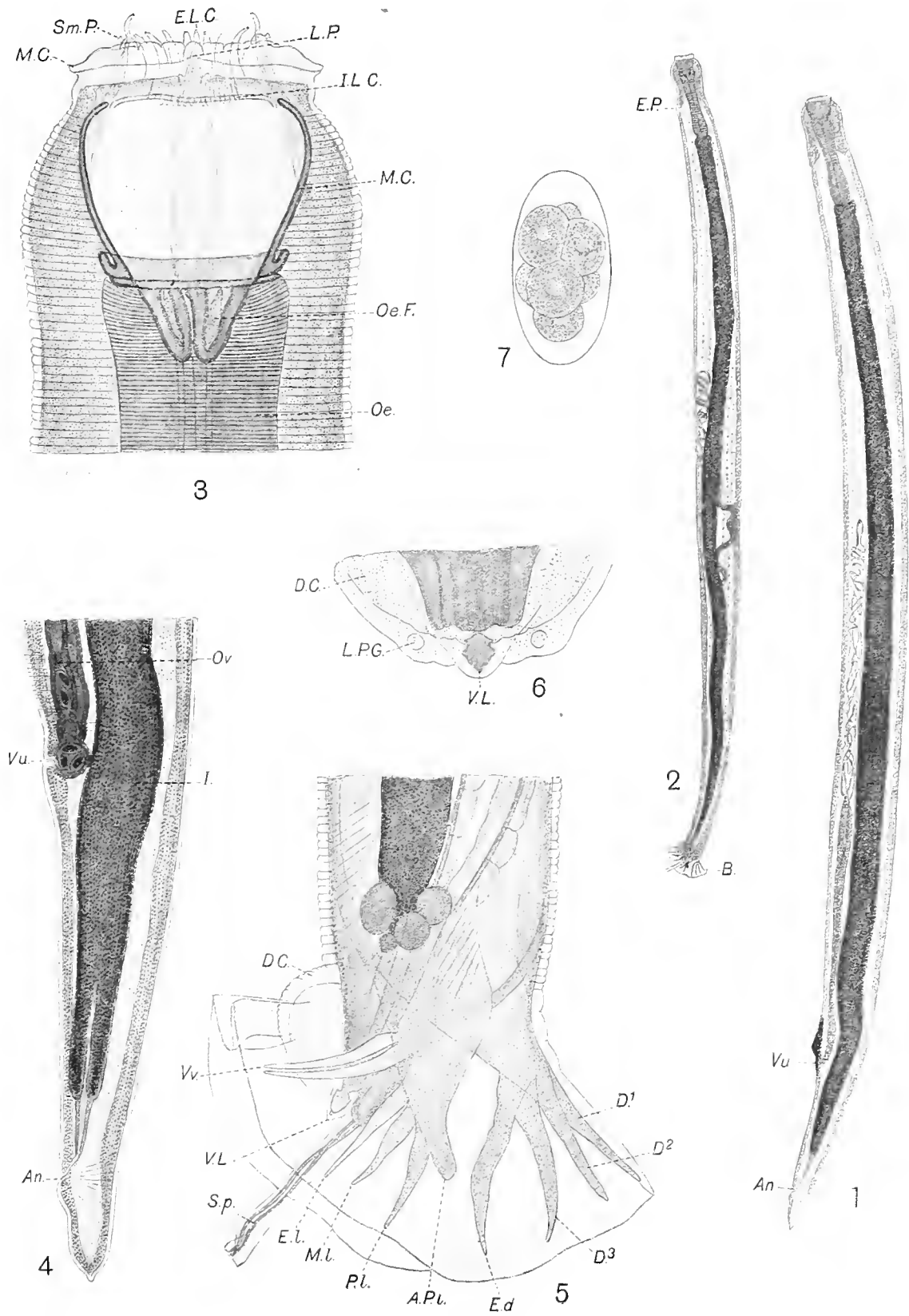
EXPLANATION OF PLATE XXII.

Oesophagodontus robustus Giles.

- Fig. 1. Female, lateral view of a specimen mounted in glycerine, $\times 8$.
- Fig. 2. Male, lateral view of a specimen mounted in glycerine, $\times 8$.
- Fig. 3. Head, lateral view, $\times 75$.
- Fig. 4. Posterior extremity of female body, lateral aspect, $\times 23$.
- Fig. 5. Posterior extremity of male body, showing lateral view of the bursa, $\times 75$.
- Fig. 6. Ventral view of the genital cone of male, $\times 120$.
- Fig. 7. Egg, from maternal uterus, $\times 225$.

INDEX TO LETTERING.

<i>An.</i>	Anus.
<i>A.P.l.</i>	Accessory branch of the postero-lateral ray of the bursa.
<i>B.</i>	Bursa of male.
<i>D¹-D³.</i>	Branches of the dorsal ray of the bursa.
<i>D.C.</i>	Dermal collar of the genital cone.
<i>E.d.</i>	Externo-dorsal ray of the bursa.
<i>E.l.</i>	Externo-lateral ray of the bursa.
<i>E.L.C.</i>	External (anterior) leaf-crown.
<i>E.P.</i>	Excretory pore.



<i>I.</i>	Intestine.
<i>I.L.C.</i>	Internal (posterior) leaf-crown.
<i>L.P.</i>	Lateral papilla of head.
<i>L.P.G.</i>	Lateral papilla of the genital cone.
<i>M.C.</i>	Mouth-collar.
<i>M.C.</i>	Mouth-capsule.
<i>M.l.</i>	Medio-lateral ray of the bursa.
<i>Oe.</i>	Oesophagus.
<i>Oe.F.</i>	Oesophageal funnel.
<i>Ov.</i>	Ovjector.
<i>P.l.</i>	Postero-lateral ray of the bursa.
<i>Sm.P.</i>	Sub-median head papilla.
<i>Sp.</i>	Spicule of male.
<i>V.L.</i>	Ventral lip of the genital cone.
<i>Vu.</i>	Vulva of female.
<i>Vv.</i>	Ventro-ventral ray of the bursa.

OBSERVATIONS ON THE HABITS AND PARASITES OF COMMON FLIES.

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(With Plates XXIII–XXX, 17 Text-figures and 9 Charts.)

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INTRODUCTION.

WITHIN the last few years several books and numerous papers have been published dealing with various problems relating to the life-histories, and disease-spreading capacities, of house-frequenting and other non-biting flies. An intimate knowledge of the habits of flies is essential if the most suitable methods are to be devised in order to diminish their numbers, yet it is only too evident that many of the accepted hypotheses are founded on the most superficial observations, and that extensive and carefully planned experiments, with a few notable exceptions, are conspicuously absent.

In 1912 the writer decided to attempt to investigate some of the problems, which have received little attention, including amongst others the wintering habits of flies, their seasonal distribution, and the succession of generations. Extensive preliminary investigations were carried out especially in the winter of 1913-14, and the summer of 1914. Flies of various species were bred from pupae, which had passed through the winter under natural conditions, flies of all species were collected daily from windows and recorded, traps of different kinds baited with various materials were used for catching flies out of doors, and records of the rainfall, barometric pressure, temperatures in various situations and daily weather conditions were kept. During the winter of 1914 the flies collected were carefully examined, and specimens of most of the commoner species were identified by Mr Percy H. Grimshaw¹, to whom the writer is very greatly indebted for all the trouble he has taken. The other observations recorded were also carefully studied, including the effects of the weather conditions.

Owing to periods of absence from Cambridge, omissions in the records, insufficient control experiments and other causes it was decided not to publish any records of these observations, but to make use of the large amount of information acquired and the experience gained in devising more elaborate investigations and experiments to be continued throughout the fly season of 1915. It was decided to attempt to ascertain the ways in which various common species pass the winter, the factors which cause different species to appear at different times, the extent to which multiplication occurs under natural conditions, the effects of varying weather conditions on different species, their habits in regard to entering houses, visiting decaying animal matter and human excrement, and certain other points of less importance.

¹ Specimens identified by Mr Grimshaw are marked *.

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While it cannot be claimed that these problems have been settled, the greatest care has been taken to render the data recorded as accurate as possible, and undoubted advances have been made towards a better understanding of the circumstances which influence the lives of flies. Experiments of the kind about to be described require continuous attention throughout the season, and are very laborious, but seem to furnish the only means by which knowledge of sufficient accuracy to be of real value for practical purposes can be gained.

THE WINTERING HABITS OF FLIES.

There has been much controversy as to the manner in which house-flies (*M. domestica*) survive the winter, some assuming that the species is perpetuated by the few which hibernate, and others that the winter is passed in the pupal stage. No very satisfactory evidence seems to have been brought forward in support of either view, though some attempts have been made to decide the question by experiment. Whatever doubt there may be about the house-fly passing the winter in the pupal stage, there can be none in regard to many of the common species which frequent the neighbourhood of houses.

In the autumn of 1912 the writer collected three samples of dog faeces and placed them in separate jars half filled with earth. The tops of the jars were closed with gauze, and the jars were put outside in a sheltered place during the winter. On March 25, 1913, the jars were examined. The first contained 110 pupae, the second 215, and the third 245, or 570 in all, of which 133 were large, 427 small and 10 of the *Fannia* type. These pupae were kept in a warm room, and from the large specimens flesh flies (*Sarcophaga melanura**) emerged between April 4 and May 9, and from the smaller *Anthomyia radicum** during the first three weeks of April.

On March 28, 1914, damp soil near a manure heap was examined, and at a depth of about three inches several large and small pupae were found. From these pupae, which were kept in a warm room, *C. erythrocephala* and one *O. leucostoma* emerged between April 4-22. In the soil close to a second heap, which was situated in an open field, a number of smaller pupae were found. From these Anthomyid flies emerged.

During the winter of 1914-15 many experiments were carried out. In October, 1914, flies were allowed to deposit their eggs on the carcasses of small animals placed on dry earth and kept in two galvanised iron

boxes¹, one (Tin I) kept in a shady, sheltered place, and the other (Tin II) in an open, sunny spot. In the latter the variations in temperature were much greater than in the former. On April 11, 1915, the pupae were collected from the "tins" and placed together with earth in wooden boxes provided with openings in the lids above which balloon traps were fitted. The two boxes were placed in the tins from which the pupae were taken, and the flies which emerged and found their way into the traps were counted daily.

From Box No. I, 987 blow-flies (*C. erythrocephala*), 489 males and 498 females, emerged between April 23 and May 11. Up to April 29 the males predominated, 107 males and 38 females emerging during that period. Later 382 males and 460 females emerged. Between April 22 and 30, 58 specimens of *F. scalaris**, 28 males and 30 females, also emerged, most of the males preceding the females. At a slightly later period, between May 10 and 20, 10 specimens, 5 males and 5 females, of *H. dentipes* emerged. Also between April 23 and May 15, 12 specimens of *Tephrochlamys canescens* appeared. From Box II only 8 males and 8 females of *C. erythrocephala* emerged between April 23 and May 2. Here again the males appeared before the females, 7 out of the 8 females emerging after all the males had appeared. The rest of the pupae were parasitised by braconids and chalcids (p. 523).

Food remains infested with fly larvae were placed in a third box in the autumn of 1914. Various species of flies emerged between April 23 and June 16—39 blow-flies (*C. erythrocephala*), 19 males and 20 females, appeared between April 23 and May 6, a few specimens of *S. carnaria* between May 6 and 10, 16 *H. dentipes* about May 20, 19 males and 16 females of *M. stabulans*, and 4 males and 6 females of *M. pabulorum* between June 5 and 16, and in the early part of May several small Anthomyids, and numerous small flies, mostly *T. canescens*.

The method just quoted was adopted in order to confine the pupae and the flies which emerged from them as much as possible, and so facilitate the recording of the results. Thinking that the conditions might be too favourable, since the pupae were protected from wet, other experiments were carried out under conditions which cannot differ materially from those which often prevail in nature. A small area of bare ground 3 × 6 ft. was enclosed by boards sunk into the earth and a cage of netting, $\frac{1}{8}$ inch in mesh, 6 feet high superimposed. Dead rabbits were placed on the ground and partly covered with leaves, and blow-flies (*C. erythrocephala*) were introduced into

¹ The construction of these boxes is described on p. 475.

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the cage together with food and water between September 1 and October 7, 1914. About 70 flies emerged during October, but no living flies were present in the cage after November 18.

Between April 29 and May 22, 1915, 308 blow-flies, 140 males and 168 females, emerged. As in an experiment previously described the males appeared at first in greater numbers than the females, 53 males and 38 females emerging between April 29 and May 6. After that date 87 males and 130 females appeared. In another open air cage of the same type 206 blow-flies emerged between April 24 and May 16, and subsequent generations were bred from them (p. 458).

In other experiments carried out in the same way in large open air cages 41 specimens of *Fannia manicata**, 26 males and 15 females, emerged between April 24 and May 10, specimens of *F. canicularis** about May 4, and 14 specimens of *Ophyra leucostoma*, 9 males and 5 females, between June 4 and 13. Eight of the nine males emerged before the first female. A pupa from the earth in this cage, brought into the house, emerged 13 days before any of those left on the ground.

It is of some interest to note that the sexes emerged in nearly equal numbers in all the experiments, for example, 656 (48.9 %) male and 684 (51.1 %) female blow-flies emerged. Another interesting point is the relatively early emergence of the males, especially in the genera *Calliphora*, *Fannia* and *Ophyra*.

During the late summer and autumn of 1914 a large number of house-flies were kept in a large gauze cage, 6 × 6 × 10 ft., erected outside on bare earth. The flies lived and bred¹ in this cage from June 21 till Oct. 9 when the last survivor died. It was hoped that some of the pupae might give rise to flies in the following year and so decide the mode of wintering of the house-fly. Unfortunately the food for the larvae was placed in depressions in the ground, and the heavy rain which fell on Oct. 15 flooded these hollows possibly causing a considerable mortality amongst the larvae. Nevertheless some living and healthy looking larvae were seen subsequently. Many of these, however, seem to have been destroyed by the heavy rain of Oct. 31, for on Nov. 4 many dead and sodden larvae and pupae were noticed amongst the remains of the food. Unfortunately also a female *H. dentipes* gained entrance and deposited her eggs. The *Hydrotaea* larvae being carnivorous doubtless destroyed many of the *Musca*

¹ As specimens caught in the house were being added frequently, it is doubtful whether any eggs were laid by flies which emerged and spent their whole lives in the cage.

larvae (p. 503). In May, 1915, a few specimens of *H. dentipes* emerged, and on Aug. 31 two house-flies were seen which seemed to be freshly emerged.

In view of the very small number of flies, the late period of the season at which they were seen, and the possibility, though small, of their having gained entrance to the eage from outside, the experiment cannot be regarded as convincing and it is being repeated under conditions which, it is hoped, will prove satisfactory.

The only other experiment of the kind carried out by Bishopp, Dove and Parman (1915) near Dallas, Texas, bears a great resemblance to the one just quoted. These observers put "about three barrels of mixed horse manure and cow manure, and straw infested with considerable numbers of larvae of all sizes and puparia into a eage" on Nov. 26, 1913.

The manure pile was covered by high water in December and no adults were seen after Dec. 27. Four adults appeared on April 16, 1914. "During the latter part of April and early May the manure was again submerged on account of heavy rains, and during this period observations were not made. It seems certain that some larvae were killed by these inundations. However, on May 26, six very vigorous adults were found in the eage. Observations on emergence were not made for some time after this."

"We thus have shown that the house-fly lived in the larval and pupal stages from Nov. 26, 1913, to May 26, 1914, a period of six months."

In order to supplement the information obtained during the previous year, similar experiments were carried out during the winter of 1915-16, in the "tins" and eages of the type described, and the larvae and pupae present were examined at various times.

In the two "tins" numerous pupae, mostly of *C. erythrocephala*, were present early in November, but many larvae continued to feed up to Dec. 31, and were seen feeding on warm days even later (Jan. 14). By Feb. 14 the larvae had left the food, and were seen amongst the pupae in the earth at the bottom of the tins. They lay still, but moved on being touched, or when light fell on them, and if brought into a warm room became quite active. On Feb. 20 many larvae and recently formed, bright coloured pupae were seen, and a few larvae were still present up to March 30. Cold weather in the autumn probably checks the feeding and growth of the larvae, but does not prevent their ultimately becoming full-fed, pupating, and emerging as flies (see p. 446). In the exposed "tin" during November and December the minimum temperature fell below 32° F. on twenty-three nights, and on one

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occasion was as low as 23° F. During November when the larvae devoured great quantities of food the mean daily minimum temperature in this "tin" was 32.4° F., the mean maximum 44.1° F.

As it was thought that the conditions in the "tins" might be abnormal the earth in an open air cage was examined. On Jan. 14, 1916, an artichoke root was pulled up with some earth attached to it. 18 blow-fly pupae and 19 larvae were found in this earth, showing that in regard to the presence of larval and pupal forms the conditions in the "tins" and in the earth were similar.

In order to determine how far down into the earth larvae make their way before pupating, a small area of the earth in the cage to the depth of 6 inches was carefully dug up and examined. Slices an inch in depth commencing from the surface were studied. In the upper inch (27 cubic inches examined) 24 pupae and 9 larvae were found, in the second inch (18 cubic inches) 5 pupae and 5 larvae, and in the third inch (18 cubic inches) only 2 larvae. Below this no larvae or pupae were found. Both the pupae and larvae were lying in definite, smooth-walled moulds, each cavity being considerably larger than the pupa or larva. On being disturbed the larvae crawled rapidly. The thirty-five larvae and forty-seven pupae obtained from the earth in the cage were placed in muslin-covered jars and kept in a warm room in which the maximum temperature reached 52° F. All the larvae soon turned into pupae and blow-flies (46 males and 33 females) emerged between Feb. 14-24. Of the remaining 3 pupae two were decomposing and one contained a braconid parasite.

Also some of the larvae in "Tin II" were separated from the pupae on December 31, 1915, and kept in a jar in the tin. In this tin blow-flies began to emerge from the winter pupae on March 19, and from the jar containing the separated larvae on April 2.

In the winter of 1914-15 very few larvae were noticed amongst the numerous pupae in the experimental "tins" and cages. In that year the mean monthly temperature recorded by a thermometer exposed on the grass gradually declined in the autumn, being 38.3° F. in October, 32.2° F. in November, and 30.0° F. in December, giving time for most of the larvae developing from eggs laid in September and October to pupate. In the autumn of 1915 on the contrary a prolonged period of cold weather occurred in November, the mean grass temperature dropping from 35.8° F. in October to 25.3° F. in November. This spell of cold weather probably checked the development of many of the late larvae. In the "tins" many of the larvae pupated under pieces

of wood, etc., without attempting to burrow into the earth. This fact in conjunction with observations on buried earcases mentioned later (p. 503) points to a tendency towards pupation within a very short distance of the surface or occasionally under shelter on the surface of the ground. That exposed pupae are not injured by low temperatures is evident from the emergence of a very large number of flies from pupae in the "tins," and outdoor cages in the spring months of 1915 and 1916 (see p. 543). The minimum temperatures recorded on the grass during the two winters were 17° F. and 12° F. In many cases the pupae lay on the top of the earth in the "tins."

These observations show that most of the common species of flies pass the winter as pupae, or less commonly as larvae, in the earth. These larvae pupate as the spring approaches, and flies emerge from them a few days later than they do from winter pupae.

The species definitely proved by experiments extending from 1912 to 1916 to be capable of passing the winter in this manner are:

<i>Calliphora erythrocephala</i> ¹	<i>Hydrotaea dentipes</i>
<i>Fannia manicata</i> *	<i>Sarcophaga melanura</i>
<i>Fannia canicularis</i> *	<i>Sarcophaga carnaria</i>
<i>Fannia scalaris</i> *	<i>Stomoxys calcitrans</i>
<i>Anthomyia radicum</i> *	<i>Mydaea lucorum</i>
<i>Tephrochlamys canescens</i> *	<i>Lucilia caesar</i>
<i>Blepharoptera serrata</i> *	<i>Lucilia sericata</i>
<i>Scatophaga stercoraria</i>	<i>Phaonia erratica</i>
<i>Dryomyza flaveola</i> *	<i>Muscina stabulans</i>
<i>Calliphora vomitoria</i>	<i>Muscina pabulorum</i>
<i>Nemopoda cylindrica</i> *	<i>Ophyra leucostoma</i>
<i>Piophilus vulgaris</i> *	<i>Poliates lardaria</i>

Observations during the winter of 1915-16 indicate, however, that a few individuals, insignificant in number compared with those passing the winter as pupae, may hibernate in the adult condition. In the perpetuation of the species these are probably of little account. Daily observations in the blow-fly cage outside showed that throughout the winter a few flies, which emerged from pupae from time to time, were present there. In January, 1916, for example flies emerged on the 10th, 18th, 21st, 26th, 28th, 29th, and 30th.

Some of these flies lived for several weeks, and survived heavy rain, snow, frost, cold winds and gales, and exhibited the most astonishing powers of resistance (see p. 465).

¹ This list is arranged according to the order in which the species have been observed to emerge, but the dates of emergence are not given since they depend on the weather conditions and vary in different years (see p. 452).

263 blow-flies, which emerged in a warm room about Jan. 1, 1916, were kept in a box with a glass front in a wooden outhouse, protected from the rain and wind. On warm days these flies became active, flew about, and took food and water which were provided for them, but during cold weather hardly moved. February was a very cold month, but by the end of it only 33 had died, and on April 4 106 (40 %) were still surviving, showing that in sheltered situations these flies can live through the winter months. In May larvae were reared from these flies.

On warm days during the winter of 1915-16 *C. erythrocephala* (on various dates), *M. stabulans* 1 ♀ (Jan. 22), *M. pabulorum* 1 ♀ (Feb. 12), *M. lucorum* 2 ♀ (Feb. 13), *E. tenax* (Jan. 1) and Anthomyid flies were noticed on the windows, and *P. cornicina* ♂ (Jan. 2), *E. tenax* ♀ (Jan. 22), *P. rudis* ♀ (Feb. 13) and several specimens of *C. erythrocephala* were caught sunning themselves in various situations outside.

The occasional occurrence of blow-flies and other species in rooms during the winter months has been recorded for years, and Copcman and Austen (1914) collected a number of species from houses in various localities during the winter of 1913-14, but came to the conclusion "that the results obtained afford no support to the belief that house-flies hibernate in this country in the adult state."

The hypothesis, strongly advocated by some writers, that the summer generations of house-flies are the descendants of hibernated or "over-wintered" females seems to be founded on the casual observations of stray flies in houses during winter time.

The writer's experiments seem to indicate that, amongst most of the common species of flies, the very great majority of individuals pass the winter as pupae, or more rarely as larvae which pupate early in the spring. The pupae or larvae are situated under shelter on the surface or are buried within two or three inches of the surface of the ground. A very small and unimportant minority of both sexes emerging from pupae late in the autumn or even in the winter possibly survive as adults till the spring. It is very improbable that many of these females are impregnated in the autumn, or that most of them reach sexual maturity much earlier than the broods emerging in the spring.

THE EMERGENCE OF FLIES FROM PUPAE.

Careful observations were made on blow-flies emerging from their puparia and the various stages are illustrated by photographs (Plate XXIII).

Further, by subjecting blow-fly pupae to different conditions an

attempt was made to ascertain the factors which determine the emergence of the flies in the spring.

The process of emergence from the puparium.

The time occupied by the various stages through which a fly passes from the moment when the puparium ruptures to the time when the fly is fully formed and normally coloured varies with the temperature. The following account of the process at 49° F. illustrates the events which occur.

Owing apparently to the pressure of the distended ptilinum within, the anterior end of the puparium suddenly ruptures, a circular split being formed near the upper margin of the fourth visible segment, or third

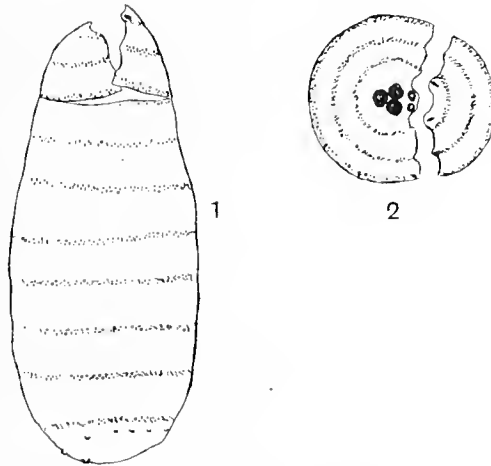


Fig. 1. Puparium of *C. erythrocephala* ($\times 5$) after the emergence of the fly, showing the mode of rupture. The circular and vertical splits dividing the cap into two approximately equal pieces can be distinguished. The remnant of one anterior spiracular process of the larva is seen as an oval black mark near the apex of the right-hand fragment of the cap.

Fig. 2. The cap viewed from above ($\times 6.5$). The remains of the anterior spiracular processes of the larva are seen on the right-hand fragment.

segment below the one bearing the remains of the anterior spiracular processes of the larva. This segment appears to correspond with the sixth segment of the larva. A vertical split also appears, and, avoiding the remains of the spiracular processes, passes through the anterior end of the puparium to join the circular split on two sides. This split divides the cap detached by the circular split into two approximately equal pieces. The splitting of the puparium seems to occur invariably in the positions just described.

In the case to be described the puparium ruptured at 12.15 p.m., and immediately the dilated, transparent ptilinum, or distensible frontal sac of the fly, appeared. It remained distended for periods of about 9 seconds, then collapsed for 2 or 3 seconds and was again distended.

Very shortly afterwards the eyes appeared. The whole head had emerged in 2 minutes, and the thorax and anterior legs were released in $2\frac{1}{2}$ minutes. The whole fly was free of the puparium in 3 minutes. All this time the ptilinum was being alternately distended and retracted¹.

At this stage the fly is a curious looking object, which the writer has been accustomed to call a "walker." It is very soft, dark grey in colour, with well-formed legs, and all its bristles and hairs are black and well developed. The lines of the bristles on its thorax are marked by darker stripes. The wings, however, are represented by opaque, narrow processes with undulating longitudinal folds, extending backwards from the thorax to the middle third of the abdomen. There is a very marked semicircular recess in the inner margin situated in the distal third of the wing. The "walker" walks about with very great rapidity, occasionally distending and withdrawing its ptilinum and presenting

¹ If the ptilinum is pricked clear fluid in large quantities is discharged from it as the fly tries to distend it.

Plate XXIII. Figs. 2-5. Puparia of *C. erythrocephala* after the emergence of the flies. (Nat. size.)

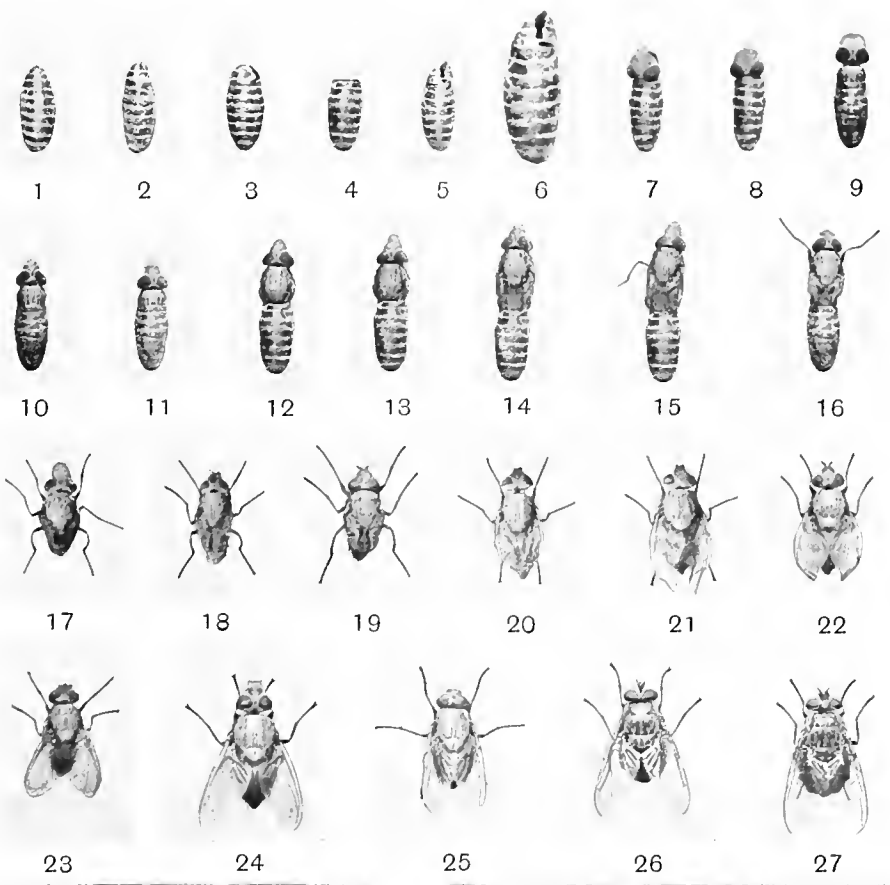
Fig. 6. The puparium illustrated in Fig. 5 enlarged.

Figs. 7-27. Photographs of living specimens of *C. erythrocephala* (nat. size) in various stages from the emergence of the head from the puparium to the mature insect. Figs. 7, 8. Head protruded from puparium and ptilinum partially distended. Fig. 9. Head and part of thorax protruded, and ptilinum much distended. Figs. 10, 11. Thorax further protruded. Figs. 12, 13. Thorax completely protruded, and folded wings visible. Figs. 14, 15, 16. The fly in the act of extricating its legs and abdomen from the puparium. Fig. 17. Early "walker" with ptilinum distended. Figs. 18, 19. Early "walkers" (ptilinum retracted). Figs. 20, 21, 22, 23. Stages in the expansion of the wings. Fig. 24. Soft grey fly with fully expanded wings, and ptilinum partially distended. Up to this stage the abdomen is markedly pointed. Fig. 25. Soft, grey, normally shaped fly. Fig. 26. Fully developed male. Fig. 27. Fully developed female. The dark longitudinal stripes marking the lines of the dorso-central bristles are distinctly visible from the moment the thorax is protruded in the puparium.

Fig. 28. Cluster of blow-flies ($\times \frac{1}{3}$) in large outdoor cage sheltering from wind in the evening.

Fig. 29. Two blow-flies ($\times \frac{1}{2}$) sunning themselves after emerging from crevices in a paling.

Fig. 30. Blow-fly ($\times \frac{1}{4}$) sunning itself after emerging from a crevice under loose-bark. Flies often select situations of the kind illustrated where they are very difficult to distinguish.



28

30



a ludicrous appearance. At this stage the ptilinum is used to help the creature to pass through earth or sand, if emergence has taken place under the soil, or through a cotton wool plug if it is confined in a test tube. The mode of procedure is to thrust the head, with the ptilinum retracted, as far forward as possible and then to distend the ptilinum so as to obtain a purchase against neighbouring particles. The body is then drawn up to the head, the ptilinum retracted, the head again thrust forward and the process repeated.

The "walker" stage lasted in this case 90 minutes, during which time the creature became much lighter in colour, assuming a light grey tint and semi-transparent appearance, and the abdomen gradually increased in size till the somewhat attenuated abdomen of the early stage had become pointed at the distal end and rounded and fully distended in its proximal parts. Then very rapidly the wings unfolded and were almost completely expanded in two or three minutes.

Shortly after the unfolding commences the wing has a crumpled appearance and the last part to expand is the tip. When first fully expanded the wings are convex when looked at from above, and have a milky-grey, opaque appearance. Within ten minutes the wings become firm and flat, though still grey and opaque, and the fly looks a soft and grey, but otherwise normal, specimen. Even at this stage the ptilinum is distended at intervals.

Three-quarters of an hour later the normal blue coloration of the fly began to appear, and the upper surface had nearly assumed the normal tint in another half hour, though the under surface was still much lighter in colour. Another hour and a half elapsed before the fly showed the typical coloration all over, though its chitin was still soft.

At 49° F. flies complete the stages described in four to five hours. After this the chitin becomes hard and no further change or growth takes place. At higher temperatures, and especially when the flies are exposed to the sun, the stages are completed very rapidly, sometimes within an hour. At lower temperatures, on the other hand, the time is very much prolonged. Occasionally the chitin may harden before the wings are expanded, leaving the fly a cripple. By removing a fly in one of the earlier stages from a warm to a cold room it may be caused to remain at the same stage of development for some hours.

In the spring months under natural conditions blow-flies usually emerge early in the morning, about 7 a.m. in April and still earlier in the warmer months. On fine days development is complete by 10 a.m.,

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but on cold, wet and sunless days "walkers" and grey flies may be found in the afternoon. In the late summer flies sometimes emerge in the evening, and in the autumn "walkers," which emerge after frosty nights, often take all day to develop into coloured flies.

Conditions influencing emergence.

Observations and experiments made in the spring months of 1915 and 1916 indicate that temperature is the factor of greatest importance in causing flies to emerge from winter pupae.

Some data for estimating the necessary temperatures are available from the records of the temperatures in the outside cage and in the "tins" during the spring of 1915. In the "tins" the daily maximum and minimum temperatures were recorded, and in the cage the maximum and minimum temperatures on the ground, in a situation shaded from the afternoon sun, and the temperature at a depth of two inches below the surface by means of a thermometer three feet long, with a protected stem, originally made for recording the temperatures in clothing during sterilization. The earth temperatures close to the cage at depths of one and two feet in exposed and shady situations were also recorded. Chart I shows in the upper part the mean daily temperature in "Tin I" in the shade and the numbers of flies of different species which emerged. Most of the pupae were lying loosely in and on the earth at the bottom, and were subjected to the influence of this temperature. It will be seen that the majority of the blow-flies emerged when the mean temperature reached approximately 48° F. and remained at or above that level, and that *F. scalaris* emerged slightly earlier. *H. dentipes* emerged a little later, possibly influenced by a decided rise of temperature of short duration between May 6 and 9, and *M. stabulans* did not emerge till the mean temperature reached 63° F.

The lower portion of the chart shows the emergence of flies in the cage and records the daily mean temperatures on the surface and at a depth of two inches, and the mid-day readings of the one foot earth temperatures in the sun and in the shade. It will be noticed that these readings are usually separated by several degrees. Most of the pupae were buried at a depth of one to two inches and were therefore subjected to the variations in temperature occurring at that level. In the cage the majority of blow-flies emerged when the mean two-inch temperature reached 48° F. and remained above that level, about a week after those in the "Tin I." *F. manicata* also appeared

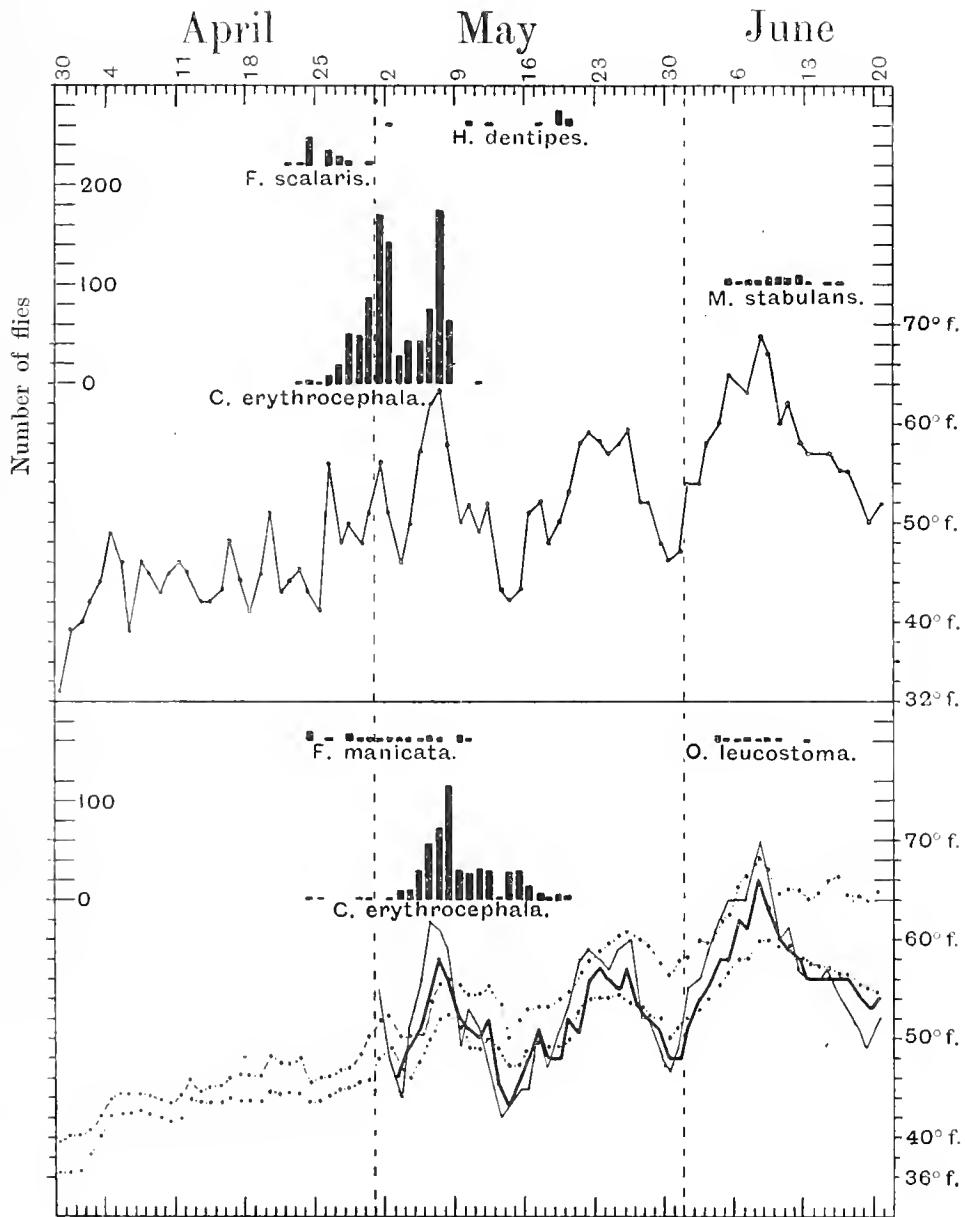


Chart I. Showing in upper part the numbers of *C. erythrocephala*, *F. scalaris*, *H. dentipes* and *M. stabulans* emerging daily from "winter" pupae, and the daily mean temperature in "Tin I" in the shade. In the lower part the numbers of *F. manicata*, *C. erythrocephala* and *O. leucostoma* emerging daily from the ground in the large outdoor eages are shown. The upper dotted line indicates the daily temperature of the ground at a depth of one foot in the open, the lower dotted line the daily temperature at a depth of one foot in the shade, the thick line the daily mean temperature at a depth of two inches in a partially shaded situation, and the thin line the daily mean temperature on the surface of the ground in the outdoor eage.

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later than *F. scalaris* in "Tin I" and *O. leucostoma* commenced to emerge when the mean two-inch temperature reached 58° F.

Forty-seven pupae and thirty-five blow-fly larvae removed from the earth in an experimental cage outside were brought into a warm room with a maximum daily temperature of 52° F. on Jan. 14, 1916. The larvae soon pupated and seventy-nine flies emerged between Feb. 14 and 24. The transference to the warmer temperature had caused the larvae to pupate, and flies to emerge in thirty to forty days. In the outdoor cage the first fly appeared on April 1. (See Table I.)

Pupae and earth taken from "Tin II" on Feb. 29, 1916 were placed in jars and kept in different rooms. Room A facing east had no fire, room B had a fire daily, and rooms C and D were warmed by the kitchen chimney and a hot-water system respectively. Room E was a kitchen. The jars, "Tins" and outside cage were examined daily, and the flies caught and recorded. The results of these experiments are given in Table I. It will be seen that in room E with a mean temperature of 60° F. flies began to emerge in five days, in rooms B, C and D in fourteen days, but not till the thirty-third day in room A. Outside they emerged earliest in "Tin II," next in "Tin I," and later in the outdoor cage with the lowest mean temperature. It will further be noticed that in all cases a mean temperature of 48° F. had prevailed for a period before large numbers emerged. In this series of experiments, except in the outdoor cage, the only varying condition was the temperature¹.

Until further evidence is available it may be permissible to put forward the tentative hypothesis that the *majority of specimens of each species* only emerge after the mean temperature of the materials in

¹ Out of doors greater daily variations in temperature occurred than indoors.

Note on Charts 1, 2, 5 and 7.

The daily mean temperature in "Tin I" and the daily mean temperatures of the earth at a depth of one foot in the open and in the shade, and at a depth of two inches in a partly shaded situation, and the daily mean temperature on the surface of the ground during April, May and June, 1915, are given in Chart 1. The daily minimum temperature on the grass, and the daily mean temperature of the earth at a depth of one foot in the shade and at a depth of two inches from April to December, 1915, are given in Chart 2. The daily maximum temperature recorded by a thermometer exposed to the sun, from May to November, 1915, is given in Chart 5. The daily maximum and minimum temperatures in the screen from May to November, 1915, are given in Chart 7.

The total daily rainfall from April to December is given in Chart 2 and the rainfall occurring in the daytime and at night in Chart 7.

The total daily hours of bright sunshine between 8 a.m. and 6 p.m., from May to November, are given in Chart 5, and the daily periods of bright sunshine in Chart 7.

which the pupae pass the winter reaches a certain point, which differs for each species.

The "critical point" for *C. erythrocephala* and for *F. manicata* and *F. scalaris* seems to be about 48–50° F., for *Ophyra* about 58° F. and for *Muscina* about 63° F.

Flies emerge from pupae in warm situations earlier than from those in shaded situations, but under natural conditions the difference in the time of emerging is probably not more than seven to ten days.

It will be noticed in Table I that after the mean temperature reaches 48° F. various periods elapse before the flies emerge. It seems probable that a temperature some degrees lower than the "critical point" is needed to produce the changes leading up to the "nymph" stage (see Hewitt, 1914, footnote p. 105). It will be noticed further that when once flies have commenced to appear they continue to emerge in spite of falls in the daily mean temperature.

In the case of *C. erythrocephala* and other flies isolated specimens emerge at various times in the winter. For instance "walkers" were seen in the outdoor cage on Jan. 21, 26, 28, 29 and 30 when the maximum temperatures on the ground were 51°, 48°, 49°, 47° and 43° F. On other occasions during the winter, especially on warm days, the numbers present had increased though the developing stages were not noticed.

It seems likely that in these cases the "nymph" stage had been reached in the autumn or sometime early in the winter, possibly owing to the pupae being in favoured situations, and that the flies were ready to emerge whenever the temperature approximated to the "critical point." It should be noted, however, that on many warm days no flies emerged.

THE MULTIPLICATION OF FLIES.

Howard (1911) (p. 37), speaking of the "possibilities in the way of numbers" of flies, makes the following statement. "The number of generations has a direct bearing upon the number of flies, not only at different periods during the summer, but also in the early autumn, since there is, barring accidents, a constant and definite and enormous increase. Of course some summers are warmer than others and some are moister than others, and upon these two factors, taken in connection with that of available places for breeding, the number of flies must depend.

"Take, for example, the possibilities in Washington, and let us estimate—on the basis of the survival of all eggs and all individual

TABLE I. *Showing the results of keeping winter pupae at different temperatures.*

1916	Outside cage		Tin' 1 in shade		Tin' 11 in sun		Room A		Room B		Room C		Room D		Room E	
Feb. 29	36 F.		38° F.		39° F.	(2) ×	46° F.		46° F.		44° F.		49° F.		59° F.	
Mar. 1	34 F.					(2) ×										
" 2	34 F.					(2) ×										
" 3	34 F.					(2) ×										
" 4	34 F.					(2) ×										
" 5	34 F.					(2) ×										
" 6	33 F.		35° F.		36° F.	(2) ×					43° F.		48° F.		60° F.	
" 7	33 F.					(2) ×										
" 8	33 F.					(2) ×										
" 9	33 F.					(2) ×										
" 10	33 F.					(2) ×										
" 11	33 F.					(2) ×										
" 12	33 F.					(2) ×										
" 13	33 F.					(2) ×										
" 14	33 F.					(2) ×										
" 15	33 F.					(2) ×										
" 16	33 F.					(2) ×										
" 17	33 F.					(2) ×										
" 18	33 F.					(2) ×										
" 19	33 F.					(2) ×										
" 20	33 F.					(2) ×										
" 21	33 F.					(2) ×										
" 22	33 F.					(2) ×										
" 23	33 F.					(2) ×										
" 24	33 F.					(2) ×										
" 25	33 F.					(2) ×										
" 26	33 F.					(2) ×										
" 27	33 F.					(2) ×										
" 28	33 F.					(2) ×										
" 29	33 F.					(2) ×										
" 30	33 F.					(2) ×										
" 31	33 F.					(2) ×										
" 32	33 F.					(2) ×										
" 33	33 F.					(2) ×										
" 34	33 F.					(2) ×										
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" 96	33 F.					(2) ×										
" 97	33 F.					(2) ×										
" 98	33 F.					(2) ×										
" 99	33 F.					(2) ×										
" 100	33 F.					(2) ×										

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Mar. 31	1	+	(1)	48° F.	+	(6)	51° F.	+	(2)	56° F.	+	(47)	51° F.	+	(5)	55° F.	+	(1)	57° F.	+	(1)	56° F.	+	(1)	55° F.	+	(1)	54° F.	+	(1)	54° F.	+	(1)	53° F.	+	(1)	52° F.	+	(1)	51° F.	+	(1)	50° F.	+	(1)	48° F.	+	(3)	43° F.	+	(2)	46° F.	+	(1)	45° F.	+	(1)	44° F.	+	(1)	43° F.	+	(1)	42° F.	+	(1)	41° F.	+	(1)	40° F.	+	(1)	39° F.	+	(1)	38° F.	+	(1)	37° F.	+	(1)	36° F.	+	(1)	35° F.	+	(1)	34° F.	+	(1)	33° F.	+	(1)	32° F.	+	(1)	31° F.	+	(1)	30° F.	+	(1)	29° F.	+	(1)	28° F.	+	(1)	27° F.	+	(1)	26° F.	+	(1)	25° F.	+	(1)	24° F.	+	(1)	23° F.	+	(1)	22° F.	+	(1)	21° F.	+	(1)	20° F.	+	(1)	19° F.	+	(1)	18° F.	+	(1)	17° F.	+	(1)	16° F.	+	(1)	15° F.	+	(1)	14° F.	+	(1)	13° F.	+	(1)	12° F.	+	(1)	11° F.	+	(1)	10° F.	+	(1)	9° F.	+	(1)	8° F.	+	(1)	7° F.	+	(1)	6° F.	+	(1)	5° F.	+	(1)	4° F.	+	(1)	3° F.	+	(1)	2° F.	+	(1)	1° F.	+	(1)	0° F.	+	(1)	-1° F.	+	(1)	-2° F.	+	(1)	-3° F.	+	(1)	-4° F.	+	(1)	-5° F.	+	(1)	-6° F.	+	(1)	-7° F.	+	(1)	-8° F.	+	(1)	-9° F.	+	(1)	-10° F.	+	(1)	-11° F.	+	(1)	-12° F.	+	(1)	-13° F.	+	(1)	-14° F.	+	(1)	-15° F.	+	(1)	-16° F.	+	(1)	-17° F.	+	(1)	-18° F.	+	(1)	-19° F.	+	(1)	-20° F.	+	(1)	-21° F.	+	(1)	-22° F.	+	(1)	-23° F.	+	(1)	-24° F.	+	(1)	-25° F.	+	(1)	-26° F.	+	(1)	-27° F.	+	(1)	-28° F.	+	(1)	-29° F.	+	(1)	-30° F.	+	(1)	-31° F.	+	(1)	-32° F.	+	(1)	-33° F.	+	(1)	-34° F.	+	(1)	-35° F.	+	(1)	-36° F.	+	(1)	-37° F.	+	(1)	-38° F.	+	(1)	-39° F.	+	(1)	-40° F.	+	(1)	-41° F.	+	(1)	-42° F.	+	(1)	-43° F.	+	(1)	-44° F.	+	(1)	-45° F.	+	(1)	-46° F.	+	(1)	-47° F.	+	(1)	-48° F.	+	(1)	-49° F.	+	(1)	-50° F.	+	(1)	-51° F.	+	(1)	-52° F.	+	(1)	-53° F.	+	(1)	-54° F.	+	(1)	-55° F.	+	(1)	-56° F.	+	(1)	-57° F.	+	(1)	-58° F.	+	(1)	-59° F.	+	(1)	-60° F.	+	(1)	-61° F.	+	(1)	-62° F.	+	(1)	-63° F.	+	(1)	-64° F.	+	(1)	-65° F.	+	(1)	-66° F.	+	(1)	-67° F.	+	(1)	-68° F.	+	(1)	-69° F.	+	(1)	-70° F.	+	(1)	-71° F.	+	(1)	-72° F.	+	(1)	-73° F.	+	(1)	-74° F.	+	(1)	-75° F.	+	(1)	-76° F.	+	(1)	-77° F.	+	(1)	-78° F.	+	(1)	-79° F.	+	(1)	-80° F.	+	(1)	-81° F.	+	(1)	-82° F.	+	(1)	-83° F.	+	(1)	-84° F.	+	(1)	-85° F.	+	(1)	-86° F.	+	(1)	-87° F.	+	(1)	-88° F.	+	(1)	-89° F.	+	(1)	-90° F.	+	(1)	-91° F.	+	(1)	-92° F.	+	(1)	-93° F.	+	(1)	-94° F.	+	(1)	-95° F.	+	(1)	-96° F.	+	(1)	-97° F.	+	(1)	-98° F.	+	(1)	-99° F.	+	(1)	-100° F.	+	(1)	-101° F.	+	(1)	-102° F.	+	(1)	-103° F.	+	(1)	-104° F.	+	(1)	-105° F.	+	(1)	-106° F.	+	(1)	-107° F.	+	(1)	-108° F.	+	(1)	-109° F.	+	(1)	-110° F.	+	(1)	-111° F.	+	(1)	-112° F.	+	(1)	-113° F.	+	(1)	-114° F.	+	(1)	-115° F.	+	(1)	-116° F.	+	(1)	-117° F.	+	(1)	-118° F.	+	(1)	-119° F.	+	(1)	-120° F.	+	(1)	-121° F.	+	(1)	-122° F.	+	(1)	-123° F.	+	(1)	-124° F.	+	(1)	-125° F.	+	(1)	-126° F.	+	(1)	-127° F.	+	(1)	-128° F.	+	(1)	-129° F.	+	(1)	-130° F.	+	(1)	-131° F.	+	(1)	-132° F.	+	(1)	-133° F.	+	(1)	-134° F.	+	(1)	-135° F.	+	(1)	-136° F.	+	(1)	-137° F.	+	(1)	-138° F.	+	(1)	-139° F.	+	(1)	-140° F.	+	(1)	-141° F.	+	(1)	-142° F.	+	(1)	-143° F.	+	(1)	-144° F.	+	(1)	-145° F.	+	(1)	-146° F.	+	(1)	-147° F.	+	(1)	-148° F.	+	(1)	-149° F.	+	(1)	-150° F.	+	(1)	-151° F.	+	(1)	-152° F.	+	(1)	-153° F.	+	(1)	-154° F.	+	(1)	-155° F.	+	(1)	-156° F.	+	(1)	-157° F.	+	(1)	-158° F.	+	(1)	-159° F.	+	(1)	-160° F.	+	(1)	-161° F.	+	(1)	-162° F.	+	(1)	-163° F.	+	(1)	-164° F.	+	(1)	-165° F.	+	(1)	-166° F.	+	(1)	-167° F.	+	(1)	-168° F.	+	(1)	-169° F.	+	(1)	-170° F.	+	(1)	-171° F.	+	(1)	-172° F.	+	(1)	-173° F.	+	(1)	-174° F.	+	(1)	-175° F.	+	(1)	-176° F.	+	(1)	-177° F.	+	(1)	-178° F.	+	(1)	-179° F.	+	(1)	-180° F.	+	(1)	-181° F.	+	(1)	-182° F.	+	(1)	-183° F.	+	(1)	-184° F.	+	(1)	-185° F.	+	(1)	-186° F.	+	(1)	-187° F.	+	(1)	-188° F.	+	(1)	-189° F.	+	(1)	-190° F.	+	(1)	-191° F.	+	(1)	-192° F.	+	(1)	-193° F.	+	(1)	-194° F.	+	(1)	-195° F.	+	(1)	-196° F.	+	(1)	-197° F.	+	(1)	-198° F.	+	(1)	-199° F.	+	(1)	-200° F.	+	(1)	-201° F.	+	(1)	-202° F.	+	(1)	-203° F.	+	(1)	-204° F.	+	(1)	-205° F.	+	(1)	-206° F.	+	(1)	-207° F.	+	(1)	-208° F.	+	(1)	-209° F.	+	(1)	-210° F.	+	(1)	-211° F.	+	(1)	-212° F.	+	(1)	-213° F.	+	(1)	-214° F.	+	(1)	-215° F.	+	(1)	-216° F.	+	(1)	-217° F.	+	(1)	-218° F.	+	(1)	-219° F.	+	(1)	-220° F.	+	(1)	-221° F.	+	(1)	-222° F.	+	(1)	-223° F.	+	(1)	-224° F.	+	(1)	-225° F.	+	(1)	-226° F.	+	(1)	-227° F.	+	(1)	-228° F.	+	(1)	-229° F.	+	(1)	-230° F.	+	(1)	-231° F.	+	(1)	-232° F.	+	(1)	-233° F.	+	(1)	-234° F.	+	(1)	-235° F.	+	(1)	-236° F.	+	(1)	-237° F.	+	(1)	-238° F.	+	(1)	-239° F.	+	(1)	-240° F.	+	(1)	-241° F.	+	(1)	-242° F.	+	(1)	-243° F.	+	(1)	-244° F.	+	(1)	-245° F.	+	(1)	-246° F.	+	(1)	-247° F.	+	(1)	-248° F.	+	(1)	-249° F.	+	(1)	-250° F.	+	(1)	-251° F.	+	(1)	-252° F.	+	(1)	-253° F.	+	(1)	-254° F.	+	(1)	-255° F.	+	(1)	-256° F.	+	(1)	-257° F.	+	(1)	-258° F.	+	(1)	-259° F.	+	(1)	-260° F.	+	(1)	-261° F.	+	(1)	-262° F.	+	(1)	-263° F.	+	(1)	-264° F.	+	(1)	-265° F.	+	(1)	-266° F.	+	(1)	-267° F.	+	(1)	-268° F.	+	(1)	-269° F.	+	(1)	-270° F.	+	(1)	-271° F.	+	(1)	-272° F.	+	(1)	-273° F.	+	(1)	-274° F.	+	(1)	-275° F.	+	(1)	-276° F.	+	(1)	-277° F.	+	(1)	-278° F.	+	(1)	-279° F.	+	(1)	-280° F.	+	(1)	-281° F.	+	(1)	-282° F.	+	(1)	-283° F.	+	(1)	-284° F.	+	(1)	-285° F.	+	(1)	-286° F.	+	(1)	-287° F.	+	(1)	-288° F.	+	(1)	-289° F.	+	(1)	-290° F.	+	(1)	-291° F.	+	(1)	-292° F.	+	(1)	-293° F.	+	(1)	-294° F.	+	(1)	-295° F.	+	(1)	-296° F.	+	(1)	-297° F.	+	(1)	-298° F.	+	(1)	-299° F.	+	(1)	-300° F.	+	(1)	-301° F.	+	(1)	-302° F.	+	(1)	-303° F.	+	(1)	-304° F.	+	(1)	-305° F.	+	(1)	-306° F.	+	(1)	-307° F.	+	(1)	-308° F.	+	(1)	-309° F.	+	(1)	-310° F.	+	(1)	-311° F.	+	(1)	-312° F.	+	(1)	-313° F.	+	(1)	-314° F.	+	(1)	-315° F.	+	(1)	-316° F.	+	(1)	-317° F.	+	(1)	-318° F.	+	(1)	-319° F.	+	(1)	-320° F.	+	(1)	-321° F.	+	(1)	-322° F.	+	(1)	-323° F.	+	(1)	-324° F.	+	(1)	-325° F.	+	(1)	-326° F.	+	(1)	-327° F.	+	(1)	-328° F.	+	(1)	-329° F.	+	(1)	-330° F.	+	(1)	-331° F.	+	(1)	-332° F.	+	(1)	-333° F.	+	(1)	-334° F.	+	(1)	-335° F.	+	(1)	-336° F.	+	(1)	-337° F.	+	(1)	-338° F.	+	(1)	-339° F.	+	(1)	-340° F.	+	(1)	-341° F.	+	(1)	-342° F.	+	(1)	-343° F.	+	(1)	-344° F.	+	(1)	-345° F.	+	(1)	-346° F.	+	(1)	-347° F.	+	(1)	-348° F.	+	(1)	-349° F.	+	(1)	-350° F.	+	(1)	-351° F.	+	(1)	-352° F.	+	(1)	-353° F.	+	(1)	-354° F.	+	(1)	-355° F.	+	(1)	-356° F.	+	(1)	-357° F.	+	(1)	-358° F.	+	(1)	-359° F.	+	(1)	-360° F.	+	(1)	-361° F.	+	(1)	-362° F.	+	(1)	-363° F.	+	(1)	-364° F.	+	(1)	-365° F.	+	(1)	-366° F.	+	(1)	-367° F.	+	(1)	-368° F.	+	(1)	-369° F.	+	(1)	-370° F.	+	(1)	-371° F.	+	(1)	-372° F.	+	(1)	-373° F.	+	(1)	-374° F.	+	(1)	-375° F.	+	(1)	-376° F.	+	(1)	-377° F.	+	(1)	-378° F.	+	(1)	-379° F.	+	(1)	-380° F.	+	(1)	-381° F.	+	(1)	-382° F.	+	(1)	-383° F.	+	(1)	-384° F.	+	(1)	-385° F.	+	(1)	-386° F.	+	(1)	-387° F.	+	(1)	-388° F.	+	(1)	-389° F.	+	(1)	-390° F.	+	(1)	-391° F.	+	(1)	-392° F.	+	(1)	-393° F.	+	(1)	-394° F.	+	(1)	-395° F.	+	(1)	-396° F.	+	(1)	-397° F.	+	(1)	-398° F.	+	(1)	-399° F.	+	(1)	-400° F.	+	(1)	-401° F.	+	(1)	-402° F.	+	(1)	-403° F.	+	(1)	-404° F.	+	(1)	-405° F.	+	(1)	-406° F.	+	(1)	-407° F.	+	(1)	-408° F.	+	(1)	-409° F.	+	(1)	-410° F.	+	(1)	-411° F.	+	(1)	-412° F.	+	(1)	-413° F.	+	(1)	-414° F.	+	(1)	-415° F.	+	(1)	-416° F.	+	(1)	-417° F.	+	(1)	-418° F.	+	(1)	-419° F.	+	(1)	-420° F.	+	(1)	-421° F.	+	(1)	-422° F.	+	(1)	-423° F.	+	(1)	-424° F.	+	(1)	-425° F.	+	(1)	-426° F.	+	(1)	-427° F.	+	(1)	-428° F.	+	(1)	-429° F.	+	(1)	-430° F.	+	(1)	-431° F.	+	(1)	-432° F.	+	(1)	-433° F.	+	(1)	-434° F.	+	(1)	-435° F.	+	(1)	-436° F.	+	(1)	-437° F.	+	(1)	-438° F.	+	(1)	-439° F.	+	(1)	-440° F.	+	(1)	-441° F.	+	(1)	-442° F.	+	(1)	-443° F.	+	(1)	-444° F.	+	(1)	-445° F.	+	(1)	-446° F.	+	(1)	-447° F.	+	(1)	-448° F.	+	(1)	-449° F.	+	(1)	-450° F.	+	(1)	-451° F.	+	(1)	-452° F.	+	(1)	-453° F.	+	(1)	-454° F.	+	(1)	-455° F.	+	(1)	-456° F.	+	(1)	-457° F.	+	(1)	-458° F.	+	(1)	-459° F.	+	(1)	-460° F.	+	(1)	-461° F.	+	(1)	-462° F.	+	(1)	-463° F.	+	(1)	-464° F.	+	(1)	-465° F.	+	(1)	-466° F.	+	(1)	-467° F.	+	(1)	-468° F.	+	(1)	-469° F.	+	(1)	-470° F.	+	(1)	-471° F.	+	(1)	-472° F.	+	(1)	-473° F.	+	(1)	-474° F.	+	(1)	-475° F.	+	(1)	-476° F.	+	(1)	-477° F.	+	(1)	-478° F.	+	(1)	-479° F.	+	(1)	-480° F.	+	(1)	-481° F.	+	(1)	-482° F.	+	(1)	-483° F.	+	(1)	-484° F.	+	(1)	-485° F.	+	(1)	-486° F.	+	(1)	-487° F.	+	(1)	-488° F.	+	(1)	-489° F.	+	(1)	-490° F.	+	(1)	-491° F.	+	(1)	-492° F.	+	(1)	-493° F.	+	(1)	-494° F.	+	(1)	-495° F.	+	(1)	-496° F.	+	(1)	-497° F.	+	(1)	-498° F.	+	(1)	-499° F.	+	(1)	-500° F.	+	(1)	-501° F.	+	(1)	-502° F.	+	(1)	-503° F.	+	(1)	-504° F.	+	(1)	-505° F.	+	(1)	-506° F.	+	(1)	-507° F.	+	(1)	-508° F.	+	(1)	-509° F.	+	(1)	-510° F.	+	(1)	-511° F.	+	(1)	-512° F.	+	(1)	-513° F.	+	(1)	-514° F.	+	(1)	-515° F.	+	(1)	-516° F.	+	(1)	-517° F.	+	(1)	-518° F.	+	(1)	-519° F.	+	(1)	-520° F.	+	(1)	-521° F.	+	(1)	-522° F.	+	(1)	-523° F.	+	(1)	-524° F.	+	(1)	-525° F.	+	(1)	-526° F.	+	(1)	-527° F.	+	(1)	-528° F.	+	(1)	-529° F.	+	(1)	-530° F.	+	(1)	-531° F.	+	(1)	-532° F.	+	(1)	-533° F.	+	(1)	-534° F.	+	(
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The periods during which the mean temperatures remained nearly constant are indicated by vertical brackets. In the case of the outside cage two mean temperatures are given, the first indicating the mean at a depth of two inches and the second (in brackets) the mean on the surface of the ground. Most of the buried pupae were subjected to temperatures between these two means. The sign + indicates an emerged blow-fly (*C. erythrocephala* or *C. vomitoria*), the sign \times a *Fannia* (mainly *F. manicata*), and the sign * braconid parasites. The figures in brackets after the signs indicate the numbers of flies which emerged daily. 81 pupae, obtained from "Tin II," were placed in room A, 131 in room B, 120 in room C, 93 in room D and 114 in room E. In these rooms no flies emerged after April 23, but braconids continued to emerge, and the records relating to them are given on p. 531. On June 2 out of the 539 pupae placed in these rooms 191 (35 %) remained intact, from which the autumn batch of braconids will probably emerge. A few of these were opened on June 2, and contained living braconid larvae.

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flies—upon plenty of places for the insect to develop and for the larvae to feed, upon an average of ten days to a generation in midsummer (this period increasing in the autumn and being greater also in the spring time), and also upon a period of ten days after emerging of the adult flies before sexual maturity is gained (this point of the duration of the existence of the adult fly before the attainment of sexual maturity has been the weak element in other calculations that have been made of house-fly abundance)—let us start then on April 15 with a single overwintering fly which on that day lays 120 eggs, and we will have the following table:

April 15th, the overwintering female lays 120 eggs.

May 1st, 120 adults issue of which 60 are females.

May 10th, 60 females lay 120 eggs each.

May 28th, 7200 adults issue, of which 3600 are females.”

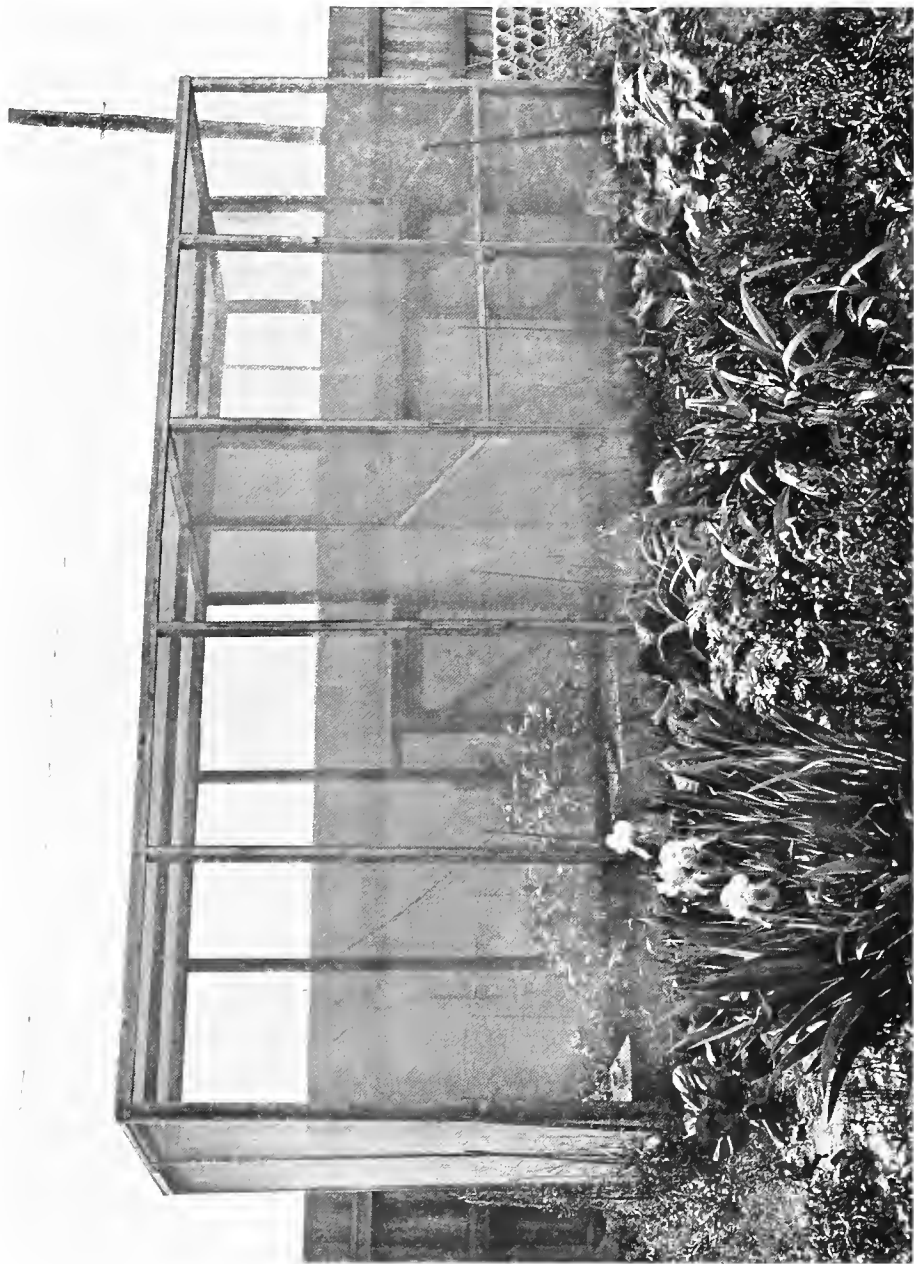
Nine further generations lay eggs on June 8, 20, July 10, 19, 29, August 8, 18, 28 and finally on

“September 10th, 5,598,720,000,000 adults issue, of which one-half are females.”

Other workers have made somewhat similar calculations and the writer decided during the seasons of 1914 and 1915 to investigate experimentally what actually occurs, since it is quite evident that multiplication under natural conditions is much more limited than such figures suggest.

For these experiments blow-flies were allowed in the autumn of 1914 (see p. 444) to deposit eggs on the carcasses of rabbits in a large open-air net cage. This cage was 6 ft. high, 15 ft. long and 6 ft. broad, with a floor of bare earth, surrounded by boards sunk into the ground (Plate XXIV). All the adults were dead by Nov. 18, 1914. Adult blow-flies commenced to emerge in this cage on April 24, 1915, the first female appearing on May 4. Altogether 206 flies emerged between April 24 and May 16. Judging by the results of a control experiment in which the flies were killed as they emerged, the sexes were in approximately equal numbers (p. 444). These flies and their descendants bred in this cage throughout the season and the flies were counted daily after they settled down for the evening with the aid of a counting machine, recording consecutive numbers after each pressure of the finger.

They were kept well supplied with food and water and dead animals to lay their eggs upon. These animals were placed in large earthenware



A large experimental cage.



pipes about six inches in diameter, half buried vertically in the ground and filled with earth up to the ground level. After a day or two, when many eggs had been deposited, the top of the pipe was covered with butter muslin over which was placed an earthenware saucer. If, on subsequent inspection, there seemed to be insufficient food for the larvae more was added. The purpose of this procedure was to confine the larvae as much as possible, and to aid in counting the numbers of the adults of the new generations as they emerged and were released from the pipes. Also the flies were prevented from laying more eggs on a given supply of food than it could nourish.

The first eggs were noted on May 15, and eggs were deposited by this generation up to June 11, when only 43 flies remained alive. The flies which emerged from the winter pupae reached their greatest number on May 15 and after that time the number present gradually diminished until on June 16 only five remained of this, the parent, generation. The flies of the first generation developing from the eggs deposited in the pipes by the parent generation only commenced to emerge on June 17, so that the parent generation had almost died off before its descendants reached the adult stage. Flies of this generation continued to emerge up to July 21. The eggs first deposited by the parent generation produced flies in 32 days.

According to Fabre the blow-fly lays about 300 eggs in one batch and therefore the first generation resulting from 100 parent females ought to have consisted, had adults matured from all the eggs deposited, of at least 30,000 individuals. The total number, which emerged under apparently most favourable conditions, was 2789.

Lack of food for the larvae was not the cause of this theoretically very small number since the bodies of numerous guinea-pigs were provided, and as shown by other observations more than 1000 flies may be bred from a single body (p. 504). Competing larvae and damp may also be excluded.

A glance at Chart 2 shows that in all the generations considerable numbers usually emerged about the same period, and the curve for the total number of flies present in consequence rises suddenly.

In most cases it also falls suddenly within a few days owing to the very great mortality which occurs amongst the newly emerged flies.

This mortality, whatever its cause, occurred regularly throughout the season and is probably one of the most important factors in limiting the numbers produced. The general causes of mortality are discussed in the next section.

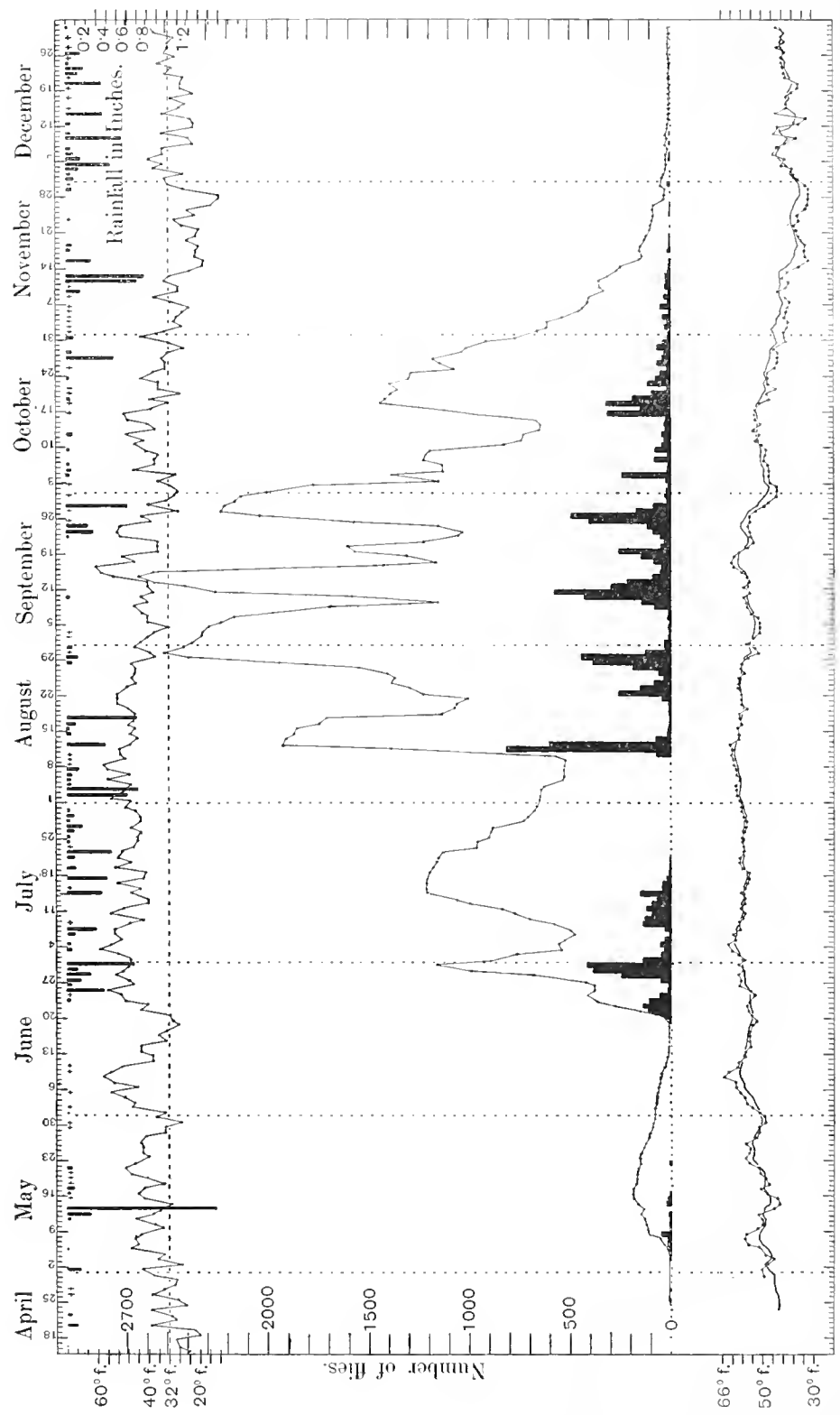


Chart 2. Showing the number of blow-flies (*C. erythrocephala*) which emerged from "winter" pupae in a large outside cage, and the subsequent generations bred from them. The black columns at the top of the chart indicate the daily rainfall (+ = traco). The daily minimum temperature on the grass is also shown at the top of the chart. The number of flies present daily is indicated by the thin line in the centre of the chart, and the number of flies emerging daily by the black columns. At the bottom of the chart the thin line indicates the daily mean temperature of the earth in the shade at a depth of one foot, and the dotted line the daily mean temperature at a depth of two inches.

The first generation laid eggs from July 12 to Aug. 6. From the first of these eggs flies emerged in 29 days. About 500 flies of the first generation were still surviving when members of the second generation began to appear on Aug. 10. This generation continued to emerge until Sept. 5, 3562 flies belonging to it being recorded. Owing to the adults belonging to two generations being intermingled it was impossible after this to be certain as to the exact numbers belonging to the succeeding generations, but the third generation began to emerge on Sept. 6 and continued to do so up to Oct. 2. About 4056 individuals belonging to this generation were counted.

Towards the end of the season 2542 flies belonging to the fourth generation appeared, and probably the majority of the pupae which hibernated in the ground through the winter of 1915-16 belonged to this generation. The descendants of the 100 females, which emerged from winter pupae, numbered during the season about 13,000 adults, instead of the 101,250,000,000 postulated in four generations by the calculation employed by Howard, or to put the matter in figures which can be more readily understood, the descendants of each female during the season numbered 130 instead of 1012 millions.

Chart 2 shows the number of living flies present on each day of the season, and the number which emerged on each day. It indicates that the flies which emerged from the winter pupae were the most hardy, for the early mortality amongst them was slight and they diminished in number gradually. In the subsequent generations, however, many of the flies only lived a few days, and probably never attained sexual maturity. Had these specimens lived longer and deposited eggs the columns representing the numbers present would probably have been several times higher.

It may be argued that this mortality amongst the young flies was due to some defect in the experimental conditions, since it does not occur amongst flies reared in captivity indoors. The conditions prevailing in such experiments are not comparable, however, to those which prevail out of doors and in natural conditions, since the effects of rain, moisture, wind, low and high temperatures, lack of food, competing larvae and other enemies are eliminated. No doubt the results would have been more convincing had it been possible to conduct two similar experiments. Such a scheme was contemplated but abandoned owing to the labour involved. To some extent however a control is provided by the numbers caught daily in the various traps (p. 483).

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Chart 4, which shows the numbers of *C. erythrocephala* caught on days selected as being the most favourable, as well as on those days which did not appear so favourable, but on which large numbers of flies were captured, resembles in many ways Chart 2 illustrating the conditions in the experimental cage.

The numbers present in both are almost identical in the early part of May; both drop to a low level at the beginning of June, both show high peaks with intervening depressions in August, September and October. The increase in numbers amongst the "wild" blow-flies, as indicated by comparing the highest peaks of these two charts, was four times smaller than amongst those in captivity. This, however, might be expected since both the "wild" flies and their larvae were exposed to many enemies such as birds, spiders, wasps, competing and carnivorous larvae of other insects, parasites etc., and to adverse conditions such as shortage of food, from which those kept in captivity were to a great extent protected.

The deep and frequent depressions in Chart 2 are not found in Chart 4, for though many deep depressions occurred in the daily record they were omitted as being possibly due to unfavourable weather conditions (see Chart 7).

These two charts exhibiting the seasonal increase amongst blow-flies, as ascertained by different methods, resemble each other sufficiently closely to warrant the belief that they afford an index of the conditions which usually prevail, and show that under natural conditions the descendants during the season of each female blow-fly, which emerges from a winter pupa, number about 130 under favourable conditions. No doubt in very favourable seasons these figures might be increased, but under no conditions could the alarming figures of Howard be remotely approached.

The descendants of the flies bred in this cage which passed the winter of 1915-16 as pupae emerged between April 1 (see Table I) and May 21, 1916. Altogether 2462 flies, 1207 ♂ and 1255 ♀, appeared. In 1916 twelve times as many flies emerged in this cage as in 1915. The experimental conditions have resulted therefore in a great increase in numbers, an increase much greater than is ever likely to occur in nature.

THE CAUSES OF MORTALITY AMONGST FLIES.

Hitherto no attempts have been made to ascertain with any degree of precision the causes of mortality amongst flies. Vague statements,

founded on casual observations, that flies die off in the autumn owing to cold and the effects of empusa disease comprise all the information that is to be found in the literature on the subject.

The only method of arriving at any satisfactory information regarding this subject is to keep flies, confined under conditions as natural as possible, and record the deaths which occur daily, and all the available meteorological data. During the summer of 1915 the writer obtained much information from the records relating to the blow-fly breeding experiment just described, and further information was obtained from observations on blow-flies which were kept in different situations during the winter 1915-16.

Before any final conclusions can be drawn such experiments will have to be repeated in order to ascertain the effects of the weather in years with differing meteorological conditions, but these observations appear to indicate that blow-flies emerging from pupae which have passed the winter in the earth are more hardy than the flies of the subsequent summer generations, and that certain individuals of the late autumn and winter generations can endure exposure to cold to an astonishing extent.

Blow-flies emerging in the spring from winter pupae.

From Chart 2 it may be seen that most of the blow-flies of the parent generation survived the very heavy rains (1.47 inches) of May 12 and 13, and that they gradually died off without a great mortality at any special period, the mean duration of life being apparently about 30 days. The spell of cold weather from May 28 to June 1 did not perceptibly increase the death-rate and most of these flies probably died of old age. Throughout the period covered by the flies of this generation the weather was on the whole fine and warm, and therefore it would be unsafe, without observations in other less favourable years, to assert definitely that the flies which emerge from winter pupae are always hardier than those of later generations.

Blow-flies belonging to the summer generations.

It will be seen from Chart 2 that after most periods of emergence a large proportion of the flies died within a few days. In the attempt to find some of the factors which contributed to this mortality charts were constructed showing the daily percentage of deaths, the total rainfall, the hours during which rain fell, the maximum temperatures in the

sun and in the screen, the minimum temperatures in the screen and on the ground, and the velocity and direction of the wind.

These charts failed to indicate any combination of weather conditions invariably associated with a high death-rate, but it was noticed that numbers of flies were often found dead on the days following heavy or continuous rain, especially during cold and windy weather. On the other hand heavy rain of short duration in mild weather was not usually associated with a high mortality.

The greatest mortality occurred on Sept. 15 and 16, very hot, oppressive and sultry days, when the flies were very lethargic, clung tenaciously to the sides of the cage and to the clothes of any one entering it, and hardly attempted to fly. Somewhat similar weather conditions prevailed on Sept. 8 and 9, and the flies behaved in the same manner, dying in great numbers. It was frequently noticed that very hot sunshine, as opposed to oppressive heat, was fatal to flies confined in traps. The insects attempted to take advantage of the shade afforded by the labels, and other parts of the traps, but many became unconscious and considerable numbers died. In the experimental cage this cause of death probably did not operate, as ample protection was afforded by the leaves of plants.

On many occasions when large numbers of flies had died the bodies were carefully examined. Among the dead were large and small, old and young specimens. The old specimens are recognisable by their frayed wings and hard chitin, and the young by their perfect appearance and soft bodies. The high death-rate which apparently occurs regularly amongst young flies, before they are sexually mature, must be an important factor in limiting the numbers of flies.

It is difficult to draw any conclusions in regard to the effects of cold, apart from rain, from the observations in the autumn of 1915 since there were few days in which some rain did not fall, and throughout the weather might be described as damp. The first cold days occurred between Sept. 26 and Oct. 4, followed by a warmer period between Oct. 5-17, but the chart continues to exhibit the same features as during the previous months. The period from Oct. 18 to the end of November was very cold and wet and the flies rapidly died off. It should be noticed however that the curve in its general shape resembles part of the curve for the second generation in July when the weather was warm. In view of the facts to be mentioned in the next section relating to the resistance of flies to cold in winter, it is open to doubt whether the late autumn mortality was not due partly to deaths from

age and partly to wet weather. The autumn mortality is more noticeable than the summer mortality because, owing to the fall in the ground temperature, few flies are emerging to replace the dead.

From the observations made in 1915, the following tentative conclusions seem permissible in regard to the natural summer generations of blow-flies; that the normal duration of life is about 30 days as judged from the observations on the first and second generations; that under natural conditions many of the newly emerged flies die within a few days; that a considerable mortality often follows wet, cold and windy days; that oppressive sultry weather is productive of the greatest mortality, and that flies are very susceptible to very hot sunshine.

Flies bred under favourable conditions indoors can be kept alive for some weeks.

Blow-flies in winter.

From Dec. 1, 1915 to the end of February, 1916, blow-flies were present in small numbers in the open-air cage. Occasional deaths occurred and solitary individuals emerged from time to time. It is unnecessary to follow the weather conditions throughout this period, or to state the numbers of flies present daily, but their resistance to adverse climatic conditions may be illustrated by the history of a few individuals during February.

On February 3 four flies, the survivors of seven which emerged between January 26 and 30, were present in the cage, and all were still alive on February 13. During this period the minimum temperature on the grass was below freezing point on nine occasions, and once fell as low as 18° F., and 0.85 inch of rain fell. On Feb. 13 three other flies emerged, and were seen in their early stages before their wings had expanded. On the same day a severe gale began, which lasted till Feb. 17, and sufficient snow fell on the night of Feb. 14 to make a considerable rent in the roof of the cage. Before this could be mended four out of the seven flies had disappeared. The remaining three flies were observed daily and lived till Feb. 28th, surviving the worst weather of the winter. During the night of Feb. 24 $7\frac{3}{4}$ inches of snow fell, the heaviest fall in the district for several years, and lesser quantities fell on three other days together with 2.48 inches of rain. On Feb. 29 one of the flies died, on March 7 another died, and the third on March 11.

These flies had very little shelter, but took advantage of the little that could be found by occasionally altering their positions from one side of the cage to the other, and survived some of the worst weather experienced here for some years.

Other blow-flies were kept under observation during this period. Flies emerging from pupae, obtained from maggots kept in a hot-house, were placed in a small box with a glass front in a wooden shed on Dec. 28. Sugar and water were provided in the box. This shed was never heated, and owing to its construction it is probable that its temperature corresponded closely with that recorded in the screen. The flies though protected from the rain and wind experienced low temperatures. All the flies, 263 in number, had emerged by Jan. 1, 1916. On cold days the flies usually remained crowded together without moving much, but were moderately active and flew about on warmer days, and were sometimes seen feeding. No deaths had occurred by Feb. 12, but 33 had died by Feb. 25. On April 4 106 (40 %) were still surviving, showing that in sheltered situations these flies can live through the winter months.

The weather conditions during February have just been stated.

From these observations we may safely conclude that blow-flies emerging in the late autumn and winter months can, even without shelter, withstand to an astonishing degree cold, rain, snow and wind, and that in sheltered situations their chances of surviving the winter are considerable.

Probably the great differences in duration of life and powers of resistance between summer and winter flies are correlated with the different degrees of activity of the insects. In summer they are extremely active, and breeding is in progress: in winter on the other hand they seldom fly, except on the warmest days, and require very little food.

FLIES ENTERING HOUSES.

Much has been written from time to time on the habits of house-flies and other species in dwelling houses, but up to the present no systematic investigation has been undertaken with the view of ascertaining under what conditions they enter houses, or the periods during which they remain in them. In order to throw some light on this subject records were kept throughout the fly seasons of 1914 and 1915 of the numbers and species of flies which entered a dining room with a large window and garden door, always kept open, facing west.

The flies were collected at intervals during the day, and killed and examined in the evening. Further, during 1915 the flies which came into the kitchen, with windows facing south, were left undisturbed, and were counted each night about 11.30 p.m. The lights in this room were

turned out about 10 p.m. and it was found that during the next hour the flies settled down for the night. In order to disturb them as little as possible the count was made with only sufficient light to see the flies satisfactorily.

Species entering rooms.

During the season many different species of flies enter rooms. It seems to be quite evident that most of the species enter by accident, but a few enter designedly with the intention of remaining indoors for longer or shorter periods. The numbers of the larger common species caught in the dining room during 1914 and 1915 are given in Table II.

During September, 1914 no records were kept and therefore the total number entering during that season is unknown.

Specimens¹ of many other species were not uncommonly found including *Psychodidae* (common), *Microchrysa polita* (few), *Sargus cuprarius* and *S. iridatus* (few), *Thereva plebeia* (few), *Syrphidae* (common), *Platystoma seminationis* (common), *Lonchoea vaginalis* (few), *Helomyza olens* (few), *Tephrochlamys canescens* (very common), *Blepharoptera serrata* (common), *Scatophaga stercoraria* (common), and *S. lutaria* (few), *Mydaea urbana*, *M. obscurata*, *M. meditabunda*, *M. impuncta*, and *M. uliginosa* (few), *Coenosia tigrina* (few), *Fannia manicata* (common), *F. armata* (few), *F. scalaris* (few), *Pegomyia bicolor* (few), *Azelia macquarti* (common), *Hydrotaea irritans* (common), *Anthomyia pluvialis* (common), *A. radicum* (few), *Phaonia variegata* and *P. erratica* (few), *Chortophila fugax* (few), *Graphomyia maculata* (few), *Musca corvina* (few), *Brachycoma devia* (few), *Phryxi vulagris* (few), *Voria ruralis* (few), *Digonochœta spinipennis* (common), and many other species less commonly.

Occasionally specimens of such species as *C. erythrocephala*, *P. erioptthalma* and *P. rudis* were found in February and March, in both years.

On examining Table II it will be seen that some species including *S. calcitrans*, *M. hortorum*, *O. cognata*, *Sarcophaga*, *M. lucorum*, *P. lardaria* and *P. albolineata* were more commonly found in 1914, which was a fine year, but *Lucilia*, *M. domestica*, *M. stabulans* and *O. leucostoma* were more common in 1915. Excluding males of *F. canicularis*, nearly twice as many females as males entered in both years.

Members of most of the species enumerated come in accidentally, remain on or near the windows, and very seldom find their way to the darker parts of the room, or go to any food which may be present. Most of their time is spent in wandering over the glass and attempting to escape. Of some of these species very few specimens enter, but of others considerable numbers come in under suitable weather conditions.

¹ Mr Percy H. Grimshaw very kindly identified specimens of all the species mentioned in this list.

Flies belonging to at least four species, *C. erythrocephala*, *S. calcitrans*, *F. canicularis* and *M. domestica*, seem to enter for various purposes.

Blow-flies, especially *C. erythrocephala*, frequently come in attracted by the presence of food in order to deposit their eggs. They will penetrate to the darker corners of the rooms and into various recesses in their endeavours to find any suitable materials on which to lay eggs, but individual specimens seldom remain long indoors, and do not seem to seek shelter in rooms.

Large numbers of *Stomoxys calcitrans* often enter in the autumn months. Though these flies occasionally attack persons in the room, their main purpose seems to be to seek shelter, for they may often be seen settled on the walls and furniture in the evenings.

The males of *F. canicularis* come into rooms in great numbers throughout the season. Unless it be for social intercourse, the reasons for this habit are not evident, since relatively few females enter and the males are little attracted to food. They spend the greater part of the day flying about, chasing and circling round one another near the ceiling, and in the evening settle high up on the walls and furniture. By catching daily all these flies in one room it was shown that varying numbers enter almost every day throughout their season. In other rooms, where they were left undisturbed, great numbers were never present, so it seems likely that there is a daily immigration and emigration and that the individuals do not remain indoors very long. Numerical estimates of the prevalence of this species in rooms based on captures in traps, on fly papers etc., are not reliable, since these flies are little attracted to the baits. In 1915 they were twice as numerous as *M. domestica* in the dining room, but their presence was hardly noticeable.

It has been stated that when the house-fly becomes common in certain rooms it displaces *F. canicularis*, causing the latter to seek upper rooms and others free from house-flies. No evidence in support of this view was obtained, for *F. canicularis* remained abundant throughout the season in the kitchen, even when house-flies were most numerous. Its habits are so unobtrusive that it is likely to escape notice when house-flies become a nuisance.

Undoubtedly the females enter rooms in smaller numbers than the males. They are less easy to identify, and so no attempt was made to ascertain their numbers, only a few being identified from time to time, but many were doubtless included amongst the 'other *Anthomyidae*' in Table II.

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The house-fly, *M. domestica*, enters dwellings more persistently than any other species, and behaves in rooms in a totally different manner to any other fly. Many specimens caught in rooms are quite soft showing that they have entered shortly after emerging from pupae. They behave in houses as if thoroughly at home, penetrating to every part of the room and seldom visiting the windows. They move about examining everything, often in a leisurely manner, feed whenever opportunity offers, are often seen mating and rest for the night on the furniture.

While other flies seem dazed in artificial light, house-flies behave in exactly the same manner as in daylight, and are not attracted to the source of the light.

In fact every circumstance of their behaviour points to design in their entry and occupation of rooms.

In 1915 house-flies first began to enter the dining room on June 6 and continued to do so in small numbers almost daily up to the end of July. It is a remarkable fact that the 15 house-flies, mostly soft, newly emerged individuals, which entered during June were all males. In 1914 five out of the first six were males. This fact tends to support the view that the house-fly passes the winter in the pupal stage, since in allied species males appear from winter pupae earlier than females (p. 444).

During July 1915, 25 house-flies, of which 17 were males and 8 females, were caught in this room, and in August 142, of which 82 were males and 60 females. In September the numbers increased considerably, but owing to the fact that the records from the 13th to the 18th are imperfect the total cannot be stated. Of those caught 90 were males and 59 females. During October the numbers increased further, 174 males and 284 females being caught in the room, but in November only 8 house-flies, 3 males and 5 females, entered the room (Chart 3).

Up to the end of September 60 % of all the house-flies entering this room were males, while in October 60 % of them were females.

The greatest numbers came in on October 8 (82) and 10 (96), both fine, but windy days.

A great difference was noticed between the behaviour of the flies in the earlier and later parts of the season. Up to the middle of September the flies seldom remained long in the room, but numbers of them flew in at the garden door and almost immediately flew out again, often without settling. During October, however, the majority of those which came in remained, settling in various places for the night.

It is stated that house-flies seldom occur in the upper rooms of houses and are apt to avoid rooms in which no food is present. During October, however, house-flies were found almost every evening settled on the walls of a bedroom above the room just mentioned. 106 were caught, of which 35 were males and 71 (67 %) females.

House-flies in the kitchen.

House-flies were first noticed in the kitchen on June 7, and though a few specimens were seen throughout that month, they only commenced to enter the room in considerable numbers on July 1. The number present daily is recorded on Chart 3. A gradual increase in the numbers occurred during July, though at this time many were probably passing in and out daily.

It will be noticed that in the middle of the season the chart bears a strong resemblance to Chart 1, recording the daily fluctuation in the numbers of blow-flies confined in an experimental cage. Each great rise in the curve probably corresponds, as in Chart 1, to the emergence of a new generation, members of which entered shortly after becoming fully developed.

The most noticeable of these rises occurred on July 30 and 31, both days with long periods of bright and hot sunshine, August 10, a very hot day, with bright sunshine at intervals, August 26, and September 5, 12 and 13 with at least 9 hours of continuous sunshine after 8 a.m., September 24, a windy day with little sunshine, and October 8, with 8 hours of continuous sunshine. These observations do not support the view that the flies enter in order to shelter from adverse weather conditions. The flies which entered on the days just mentioned usually appeared to leave the room in small numbers daily, ten days or more elapsing before the incursion of a fresh swarm.

On seven days, varying greatly in regard to weather conditions, considerable numbers of flies emigrated out of the room; August 3, a very wet day, August 13 and 31, very bright, warm, sunny days, September 14 a dull day with a strong west wind, September 15 a hot and sunny day, September 30 a cold and sunless day and October 18th a mild and sunless day.

During the course of these observations the impression was created that the members of each swarm remained indoors for varying periods, and that in the periods between the swarms little immigration took place.

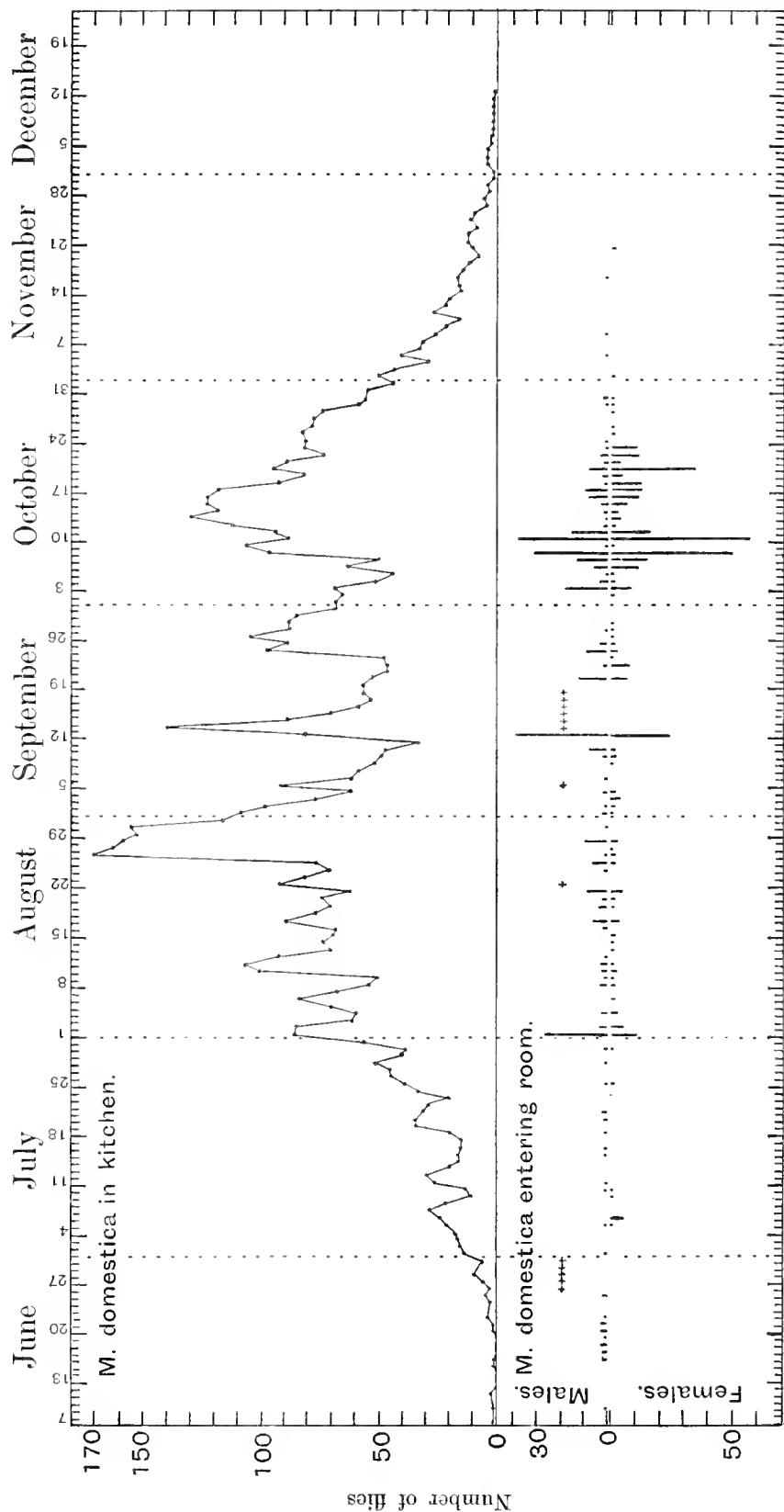


Chart 3. Showing the number of house-flies present each evening in the kitchen, and the numbers daily entering a dining room facing west. On days marked + the sexes of the flies caught in this room were not determined.

After October 25 it is improbable that many flies entered, and the numbers present gradually decreased till all had disappeared on Dec. 12.

In order to obtain some more definite information on this point 31 house-flies, caught in another room, were marked with yellow chalk and liberated in the kitchen on August 23. Only one was found there next day, and two specimens were found in other rooms in the house. The others had disappeared. The process of marking seemed to have such a disturbing effect on the flies that as a means of investigating their habits the method was abandoned.

Possibly the development of the ova requires a high temperature and the flies remain until they are ready to lay their eggs, which seem never to be deposited on food in kitchens.

In Jepson's (1909) "observations on the breeding of *Musca domestica* during the winter months" no mention is made of the finding of eggs or larvae in the very hot bake-house and sculleries where the adults were found, though experimentally they could be induced to oviposit.

Useful information might be obtained by keeping adult house-flies at various temperatures in order to ascertain whether impregnation and the development of the ova within the female are inhibited below certain temperatures. It was noticed (p. 508) that house-flies kept outside in cages laid very few eggs, suggesting that the temperature conditions were unfavourable.

Such experiments might furnish the explanation of the flies' habit of entering and remaining in warm rooms.

OBSERVATIONS BY MEANS OF TRAPS ON THE FACTORS INFLUENCING THE OUTDOOR HABITS OF FLIES.

Purposes of the investigations.

During the summer of 1914 a large number of preliminary observations on the habits of various flies by means of traps were undertaken with the intention of gaining experience in the most suitable methods for conducting more extensive investigations in 1915. It was noticed that the forms and situations of the traps, the baits, the weather and the period of the season all exerted marked influences.

The observations about to be described were made in a garden, 50 yards long and 14 yards wide, adjoining on the north a cultivated garden, on the west a large school playing field surrounded by cultivated fields, on the south an uncultivated patch of ground and on the east

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the house. About two-thirds of the area of the garden was occupied by a lawn and the rest by flower beds, etc. (Plate XXV).

The purposes of these observations were to ascertain the numbers and kinds of flies attracted throughout the season to fresh human excrement, to the carcasses of small animals, and to fruit, the results of placing these baits in darkness, in the shade and in the open, and the effects of varying weather conditions. These experiments were supplemented by catching and examining "wild" flies and observing their habits.

Daily records of the maximum and minimum readings of earth thermometers, at depths of two inches and of one and two feet, in the open and in the shade, of a thermometer placed on the grass, of a thermometer exposed to the sun, and of thermometers placed in the two galvanised iron traps (p. 475) were kept. The quantities of rain falling during the day and night were separately recorded and notes made as to the direction and strength of the wind, and the general weather conditions. The writer is greatly indebted to Mr R. I. Lynch for allowing him to make use of the daily sunshine charts obtained at the University Botanic Gardens, and to Messrs W. E. Pain and Sons for records of the mean daily velocity of the wind.

Open traps, constructed of mosquito net.

A very satisfactory, easily constructed and cheap form of trap, into which all the species attracted by the baits enter readily, is made in the following way. The base consists of a light, wooden framework 18×18 inches. A strong galvanised iron wire runs through each corner and projects downwards two inches below the wooden framework. These projections are forced into the ground and help to fix the trap. Above the framework the wires are carried vertically upwards for six inches. At this point they are bent inwards, and carried upwards for six inches to be inserted into the four corners of a square piece of wood 6×6 inches with a round hole, three inches in diameter, cut in the centre.

At the level of the bend just described a wire is carried round the trap. This wire is fixed to the vertical portions of the four corner wires. On the lower wooden framework four wires are fastened parallel, but four inches internal, to the four sides. The intersections of these wires enclose an area ten inches square. Mosquito net, $\frac{1}{8}$ inch mesh, is sewn round the upper sloping portion of the wire frame and fixed by laths to the upper square piece of wood. From the encircling wire the



Photograph of the garden in which the experiments were conducted. *A* marks the position of trap V, baited with animal remains; *B* of trap II in the shade baited with excrement, *C* of the position of trap I in the open baited with excrement, *D* of trap IV in the open baited with animal remains and *E* of the dark trap III baited with excrement.



net is carried inwards and downwards and sewn to the intersecting wires, leaving the square area just mentioned uncovered. Over the circular hole in the upper piece of wood a balloon trap is fixed, and the bait is contained in a shallow earthenware saucer placed in the square uncovered area at the base of the trap (Figs. 3 and 5). In these traps the bait is exposed in as natural a manner as possible.

Flies attracted by the bait easily find their way to it, being directed by the inward slope of the lower part of the net. After leaving the bait they tend to fly upwards and outwards and strike the inner sides

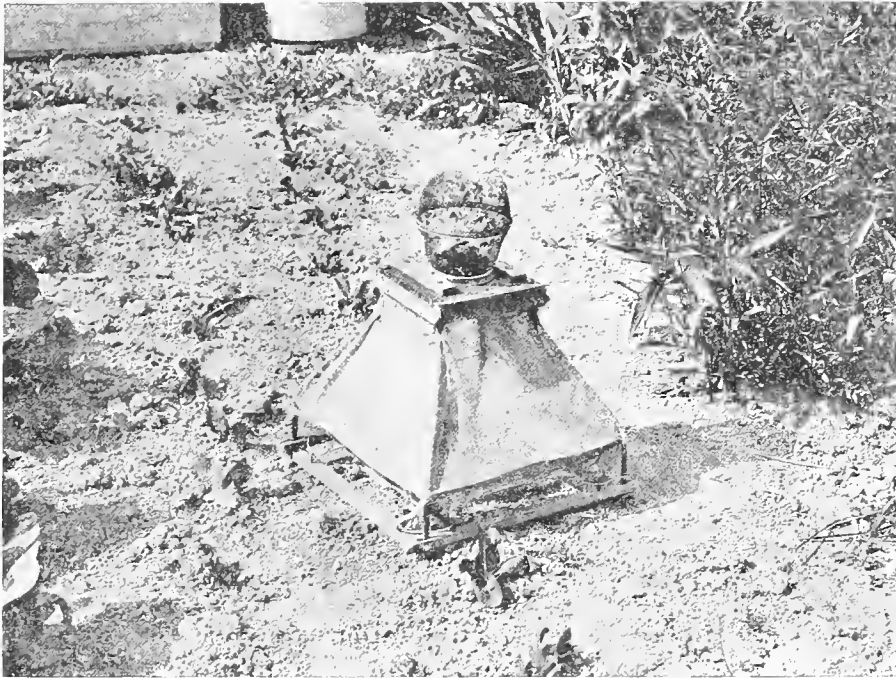


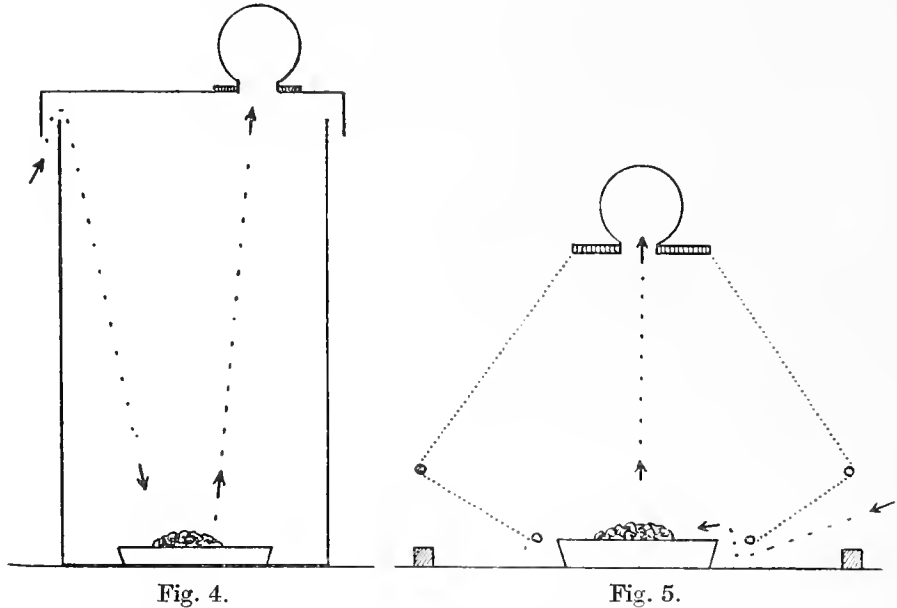
Fig. 3. Open mosquito-net trap.

of the trap. The lower inward slope just mentioned prevents their finding the entrance, and most of them move up the sides and soon enter the balloon trap.

Galvanized iron traps, or "tins."

This trap resembles one constructed by Prof. C. F. Hodge, and consists of a circular galvanized iron box 2 ft. high and 1 ft. in diameter. The lid, with a rim 3 inches in depth, projects 2 inches beyond the upper margin of the box, and is supported on flanges so that the flies can pass up between the rim of the lid and the box and gain entrance into

the interior, where the bait is placed. In the lid is a circular hole over which a balloon trap is fitted. Except for the small amount of light entering by the hole just mentioned the interior is in darkness, and the flies which gain entrance are attracted, when they desire to leave the bait, to the light and pass into the balloon trap. Only species willing to enter dark places will be caught in these traps. For the sake of brevity these traps are spoken of as "tins."



Figs. 4 and 5. Illustrating the structure of (4) the galvanised iron trap and (5) the mosquito-net trap. The arrows indicate the directions taken by the flies in entering the traps and passing into the balloons after leaving the baits.

Situations of the traps and baits employed.

Traps baited with human excrement.

I. A net trap, baited daily with fresh human excrement, was placed on soil in an open situation to ascertain the numbers and species of flies visiting this material in an exposed and sunny place (Fig. 3).

II. A net trap, baited daily with fresh human excrement, was placed on soil in a very shady place on the north side of a wooden paling running east and west, about 50 feet from trap I, to ascertain the species visiting excrement in shady places (Plate XXV, *B*).

III. A "tin" trap, baited daily with fresh human excrement, was placed in an open situation protected from winds, and from the afternoon sun, to ascertain the species attracted to such material in a dark receptacle (Plate XXV, *F*).



Fig. 2. Trap V.



Fig. 1. Trap VI.



Traps baited with decomposing animal matter.

IV. A net trap, baited weekly with the bodies of guinea-pigs and other small animals, was placed in an open situation, about 50 ft. from trap I, on the south side of a paling running east and west, to ascertain the species and numbers of flies visiting decaying animal matter in the open (Plate XXV, *E*).

V. A "tin" trap baited with bodies of small animals was placed in a very shady situation, to ascertain the species attracted to animal matter in a dark receptacle in the shade (Plate XXV, *A*, and Plate XXVI, fig. 2).

VI. A "tin" trap baited with bodies of small animals was placed in an open sunny situation, to ascertain the species willing to pass into a dark receptacle in the open (Plate XXV, *D*, and Plate XXVI, fig. 1).

Trap baited with fruit.

VII. A net trap, baited with fruit of various kinds, was placed in a similar situation to trap IV, but about 60 feet distant from it, to show the species visiting over-ripe fruit.

Observations by means of traps I–VI were commenced on April 11, but trap VII was not baited till Aug. 2. The balloon traps were brought in every evening, and the flies killed by chloroform, examined and recorded.

In order to gain further information on the habits and prevalence both of species which entered the traps and of those which are common, but are not attracted to the baits used, flies of various kinds were caught on flowers, palings, etc., for at least an hour daily during the warmest time of the day. Also during the fruit season flies which visited plums and other fruit, either still hanging on the trees or lying on the ground, were collected on several occasions in orchards.

Common species of flies found out-of-doors.

The larger flies, which frequent gardens and are attracted to human excrement and decaying animal matter, belong to a limited number of species, but most of them possess no popular names, and are only described in entomological journals. In order to help those who may be interested in this subject, photographs of living specimens of most of the commoner species are reproduced life-size in Plate XXVII.

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The writer¹ has published short descriptions with enlarged drawings of several of these species, namely *C. erythrocephala*, *C. vomitoria*, *L. caesar*, *M. domestica*, *P. rudis*, *M. stabulans*, *S. calcitrans*, *F. canicularis*, *S. carnaria*, *S. stercoraria*, to which the reader is referred.

Of the other species figured in Plate XXVII short descriptions are given in the following pages.

Phormia groenlandica Ztt.

A large, strongly built, shining, dark blue fly, nearly as large as the blow-fly, but not so stout.

Length. 10 mm.; span of wings 22 mm.

Head. The eyes are dark red, and separated, in the male by a distance of 0.5 mm., in the female by 1.25 mm. The frontal region and cheeks are black. Antennae dark; arista feathered on both sides except the terminal fourth. Palps yellow.

Thorax. Dark blue with some very poorly marked longitudinal stripes. Dorso-central bristles absent. The mesonotum is distinctly flattened just behind the transverse suture.

Wings. Clear, with fourth longitudinal vein curved up towards the third. Squama yellow.

Legs. Black.

Abdomen. Blue.

Protocalliphora azurea Fln., a much rarer fly, closely resembles *P. groenlandica* in size and appearance, but the eyes on the male are closer together (separation 0.25 mm.) and the bristles on the thorax are strongly developed. Only two males and two females of this species were caught during the season.

Pyrellia eriophthalma Mcq.

A rather large, dull-green fly, slightly smaller than *Lucilia*.

Length. 9 mm.; span of wings 18 mm.

Head. Eyes in the male very close, in female separated by 1 mm. Frontal region and cheeks dark. Antennae black. Arista feathered above and below from tip to one-third from proximal end, where the lower feathers cease.

Thorax. Dark dull green with grey stripes in anterior portion. Inner post-sutural dorso-central bristles, one near abdomen; outer dorso-central, four.

Wings. Slightly yellow, with fourth longitudinal vein curved up towards the third. Squama yellow.

Legs. Black.

Abdomen. Dark green.

¹ Graham-Smith, G. S. (1914). *Flies in relation to disease. Non-bloodsucking flies.* Cambridge University Press.

Pseudopyrellia cornicina Fab.

A bright, metallic green fly, smaller than *P. eriophthalma* and less elongated in appearance.

Length. 7 mm.; span of wings 15 mm.

Head. In male eyes separated by 0.3 mm., in female by 1.2 mm. In both sexes the frontal stripe is black and narrow and bordered by bright green bands; cheeks bright green. Antennae black. Arista feathered as in *P. eriophthalma*.

Thorax. Bright green without stripes. Inner post-sutural dorso-central bristles, one near abdomen; outer dorso-central bristles, three.

Wings. Clear with fourth longitudinal vein turned up towards the third. Squama white.

Legs. Black.

Note. *P. eriophthalma*, *P. cornicina* and flies belonging to the genus *Lucilia* resemble each other in being green coloured. Besides differences in shape, antennae and coloration, the dorso-central bristles

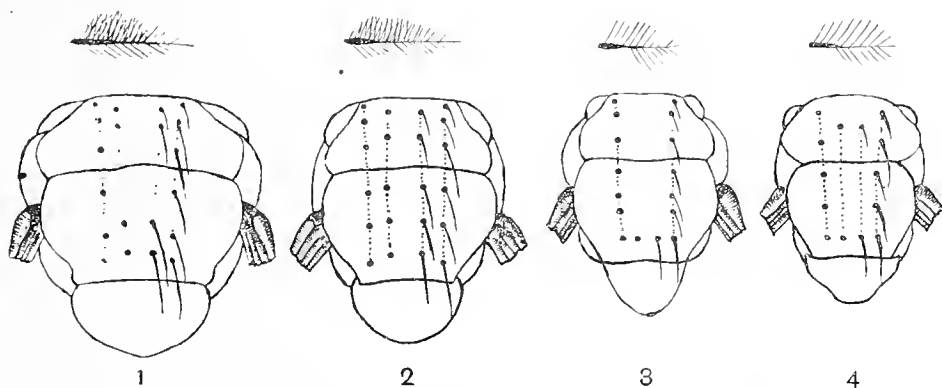


Fig. 6. Diagrams of the dorsal surface of the thorax of (1) *L. caesar*, (2) *L. sericata*, (3) *P. eriophthalma* and (4) *P. cornicina*. The sites of attachment of the dorso-central bristles are shown on the left and the bristles on the right. The arista of the antenna is shown above in each case.

afford easy distinguishing marks. Their arrangement in the first two species has just been described. In the group to which *L. caesar* belongs there are two post-sutural inner dorso-central bristles, and in the group to which *L. sericata* belongs there are three.

Graphomyia maculata Scop.

A large, grey fly with black sharply defined markings. The male is much darker than the female.

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Length. 9 mm.; span of wings 20 mm.

Head. In the male eyes separated by 0.2 mm., in female by 1.25 mm. Frontal stripe black; the frontal margin of the eyes and face white. Antennae black and arista feathered on both sides except near tip.

Thorax. Four broad black bands run backwards to middle of thorax, and a black diamond-shaped mark stretches over the posterior part of the thorax and base of the scutellum.

Wings. Clear with fourth longitudinal vein curved upwards towards the third. Squama white.

Legs. Dark grey.

Abdomen. Grey and black with distinct chequered appearance.

Muscina pabulorum Fln.

Resembling *M. stabulans* in appearance, but larger and with more distinctly defined dark markings on the thorax and abdomen. The legs also are dark.

Mydaea lucorum Fln.

A brown fly rather larger than the house-fly, *M. domestica*.

Length. 7 mm.; span of wings 16 mm.

Head. Eyes in the male almost touching, in the female separated by 1 mm. Frontal stripe in female grey, and frontal margins of eyes white. Antennae black. Arista feathered above and below.

Thorax. Brown with irregular and ill-defined dark stripes and markings.

Wings. Clear, but anterior and posterior cross veins have diffuse brown areas around them. The fourth longitudinal vein passes straight outwards to the edge of the wing. Squama yellow.

Legs. Dark brown.

Abdomen. Brown with dark spots.

Polyetes lardaria Fab.

A very large, grey fly, bearing a superficial resemblance to *S. carnaria*.

Length. 10 mm.; span of wings 24 mm.

Head. Eyes in male almost touching, in female separated by 1.25 mm. Frontal stripe is black, and the frontal margins of the eyes and face pale yellow. Antennae dark grey and arista feathered above and below.

Thorax. Grey with dark longitudinal stripes, well-defined in front, but less well-defined further back.

Wings. Clear and large. Fourth longitudinal vein runs straight out to the margin of the wings. Squama white.

Legs. Dark grey.

Abdomen. Grey and black with distinct chequered appearance.

Hydrotaea dentipes Fab.

A very common, dark brown fly, about the size of the house-fly, *M. domestica*, and probably often mistaken for that species. The male is much darker than the female.

Length. 8 mm.; span of wings 16 mm.

Head. In the male eyes close together, separated by 0.2 mm.; in female separated by 1 mm.; frontal stripe black and frontal margins of eyes white; antennae black. Arista bare.

Thorax. In male almost uniform dark brown; in female brown with dark stripes, ill-defined except near the head.

Wings. Smoky in male, clear in female. The fourth longitudinal vein runs straight out to the margin of the wing. Squama white.

Legs. Dark. The front femur of the male bears a tooth-like downward projecting spur, and a tubercle on its under surface about 0.3 mm. from its distal end.

Abdomen. Dark brown with irregular darker markings.

Ophyra leucostoma Wied.

A medium-sized, blue-black fly. The male is usually distinctly larger than the female.

Length. 7 mm.; span of wings 15 mm.

Head. The head of the male is very large and the eyes very close together. The head of the female is smaller and the eyes separated by 0.75 mm. Frontal region black. Antennae black. Arista bare.

Thorax. Shining blue-black without markings.

Wings. Clear with fourth longitudinal vein passing straight out to the margin of the wing. Squama almost transparent.

Legs. Black.

Abdomen. Shining blue-black.

Plate XXVII. Photographs of living specimens (nat. size) of common species of flies.

Except in figs. 6, 7, 19 and 20 both sexes are shown, the male on the left and the female on the right. The left wing is illustrated also to show the venation.

- | | |
|--|--|
| Fig. 1. <i>Phormia groenlandica</i> Ztt. | Fig. 12. <i>Musca domestica</i> L. |
| „ 2. <i>Calliphora erythrocephala</i> Mg. | „ 13. <i>Sarcophaga carnaria</i> L. |
| „ 3. <i>Calliphora vomitoria</i> L. | „ 14. <i>Mydaea lucorum</i> Fln. |
| „ 4. <i>Lucilia sericata</i> Mg. | „ 15. <i>Poecilodes lardaria</i> Fab. |
| „ 5. <i>Pseudopyrellia cornicina</i> Fab. | „ 16. <i>Hydrotaea dentipes</i> Fab. |
| „ 6. <i>Pyrellia criophthalma</i> Macq. (♀). | „ 17. <i>Ophyra leucostoma</i> Wied. |
| „ 7. <i>Graphomyia maculata</i> Scop. (♀). | „ 18. <i>Fannia canicularis</i> L. |
| „ 8. <i>Pollenia rudis</i> Fab. | „ 19. <i>Scatophaga suilla</i> Fab. (♂). |
| „ 9. <i>Muscina stabulans</i> Fln. | „ 20. <i>Dryomyza flaveola</i> Fab. (♀). |
| „ 10. <i>Muscina pabulorum</i> Fln. | „ 21. <i>Eristalis tenax</i> L. |
| „ 11. <i>Stomoxys calcitrans</i> L. | |

Dryomyza flaveola Fab.

A long, yellow fly bearing a superficial resemblance to *S. stercoraria*.

Length. 11 mm.; span of wings 21 mm.

Head. Yellow. Eyes in both sexes widely separated (1.25 mm.), antennae yellow.

Arista bare.

Thorax. Yellow, with darker longitudinal stripes. Strong black bristles laterally, but inner and outer dorso-centrals one and two respectively, near scutellum.

Wings. Very long and clear.

Legs. Pale yellow.

Abdomen. Pale yellow, with long pale hairs on hinder margins of segments.

Eristalis tenax L. The Drone-fly.

A very large fly resembling a drone bee. Variable in its coloration. The peculiar venation of the wings should be noticed. This fly does not visit excrement or decaying animal matter, but it is common in gardens and is found not infrequently on windows.

Other species occurring rather less commonly are *Musca corvina*, *Morcellia hortorum*, *Onesia cognata*, *Polietes albolineata*, *Phaonia erratica*, *Platystoma seminationis*. Small numbers of many other species are found.

SEASONAL DISTRIBUTION AND ABUNDANCE OF SPECIES.

From the various records obtained it has been possible to construct Chart 4 which probably gives an approximately accurate representation of the prevalence of the various common species in the neighbourhood of Cambridge during the year 1915. Similar charts compiled for other years would probably show slight differences both as to numbers and times of relative abundance, but the preliminary observations of 1914 indicate that the variations would be small except in years with very abnormal climatic conditions.

In constructing this chart the daily weather records were first inspected and the most favourable days for flies selected. The numbers of each species caught on these days or on other apparently less favourable days when very large numbers occurred are represented as columns, and the tops of these columns joined to give a curve representing the fly population.

A comparison with Charts 2 and 3 shows that the higher peaks probably represent recently emerged specimens of fresh generations,

and the depressions the periods intervening between generations when many of the flies die.

Before considering the species in detail certain general features of the chart may be discussed.

The observations already described (p. 442) on the wintering habits of flies show that from batches of pupae in certain situations most of the adults emerge within a few days of each other, though isolated individuals emerge before the majority. When plotted in the form of a chart this mode of emergence produces a rapid rise in the curve at an early period. This is well illustrated in the curves for *C. erythrocephala*, *Lucilia*, *M. stabulans*, *H. dentipes*, *O. leucostoma* and the small *Anthomyidae*.

It has also been suggested that the period of emergence is dependent on the rise of the ground temperature to the "critical" point for each species. If this view is correct a species requiring a relatively high temperature for emerging would tend to disappear early, since after the temperature falls below the required level in the autumn no further flies are likely to emerge to replace those which were dying off. Species on the other hand with a low "critical" temperature would go on emerging later. In the chart it will be noticed that the late emerging species such as *P. groenlandica*, *Lucilia*, *M. stabulans*, and *O. leucostoma* were the first to disappear, whereas those which appeared earliest, such as *C. erythrocephala*, *S. calcitrans*, disappeared late. Certain species with peculiar habits seem to be exceptions to this rule.

The conditions, which limit the numbers of a species, are various, and up to the present have been insufficiently studied. Among the more important are the destruction of larvae and pupae by braconid and chalcid parasites (p. 523) and other enemies, lack of food for the larvae owing to the eggs being deposited in great numbers on material insufficient to nourish all the larvae which develop (p. 504), the larvae of certain species devouring those of other species, the attacks of enemies of the adult flies, and weather or other conditions causing great numbers of the freshly emerged flies of each generation to die. All these factors, and probably others at present unknown, operate with varying effect in different seasons and at different places.

Experiments with blow-flies have been described and consequently the curves of *C. erythrocephala* and *C. vomitoria* need not be discussed. *Phormia groenlandica* seems to be considered a rare species (Austen, 1909), but in the neighbourhood of Cambridge it is moderately common. One hundred and thirteen were caught in traps alone in 1915, and

examples were noticed on many occasions in different localities in the neighbourhood. It appeared early in June, was most abundant in September and disappeared at the end of October.

Flies of the genus *Lucilia* appeared early in May, and were very abundant at the end of August and beginning of September. Towards the end of September their numbers diminished very rapidly.

Pyrellia eriophthalma is never abundant and has a peculiar seasonal distribution. Single specimens are not uncommonly found in February and March, and moderate numbers in May and June. After this time very few specimens are found till the late autumn, when it is not very uncommon.

Pseudopyrellia cornicina appears late, occurring in small numbers from June to September, but not becoming abundant until October.

Pollenia rudis was not uncommon in the early spring and in the autumn, but was rare in the summer. These insects rarely visit traps except those baited with fruit. Keilin (1915) has shown that its larvae develop in the earthworm, *Allolobophora chlorotica*.

The habits and distribution of *M. domestica* have been dealt with in detail (p. 470). Only two were caught in traps baited with excrement and animal matter throughout the year.

Musca corvina was not uncommon in the spring and occurred in small numbers throughout the late summer months. In Surrey it was very abundant during April. This insect was seldom caught in the traps.

Solitary examples of *Muscina stabulans* were caught throughout May, but the majority only emerged in June (p. 452). It was moderately abundant throughout the summer. *M. pabulorum* is less common but has the same seasonal distribution.

Morellia hortorum appeared towards the end of May and disappeared in the middle of October.

Stomoxys calcitrans began to appear in small numbers early in April, was common throughout the summer, and most abundant early in October. This insect never visits traps.

Members of the genus *Sarcophaga* were most abundant in June and August, but were caught in small numbers from May to November. They were more abundant in 1914.

Onesia cognata was very uncommon in 1915, but was abundant in 1914. Keilin (1915) has discovered that the larvae of this species are parasitic in earthworms.

Hydrotaea dentipes was one of the most abundant flies throughout

April May June July August September October November
 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31

Calliphora erythrocephala.

Calliphora vomitoria.

Phormia grœnlandica.

Lucilia.

Pyrellia eriopteralma.

Pseudopyrellia comicina.

Pollenia rudis.

Musca domestica.

Musca corvina.

Muscina stabulans.

Muscina pabulorum.

Morellia hortorum.

Stomoxys calcitrans.

Sarcophaga.

Onesia cognata.

Hydrotaea dentipes.

Pollia lardaria.

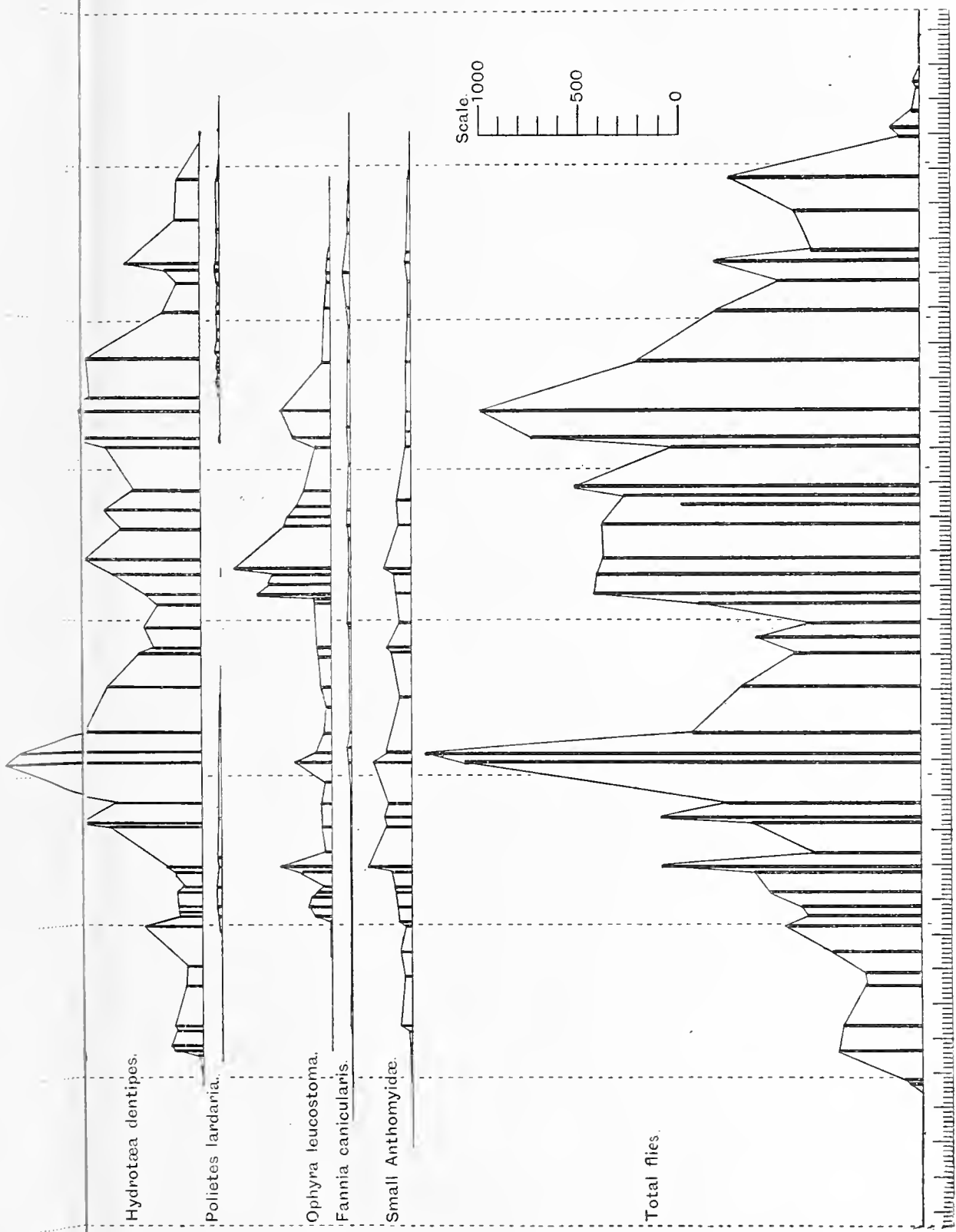


Chart 4. Showing the seasonal distribution and abundance of common species of flies at Cambridge during the season of 1915.



the season. Owing to the carnivorous habits of its larva this insect is an important agent in limiting the numbers of other flies (p. 503).

Polietes lardaria occurred in moderate numbers in June and in the autumn. In both 1914 and 1915 it was very scarce in July and August.

Ophyra leucostoma was abundant from June to October, the greatest numbers occurring in August.

The males of *F. canicularis* entered the house in considerable numbers from May to October.

The last curve shows the combined seasonal distribution of all the species caught in the various traps.

Numbers of flies caught in traps.

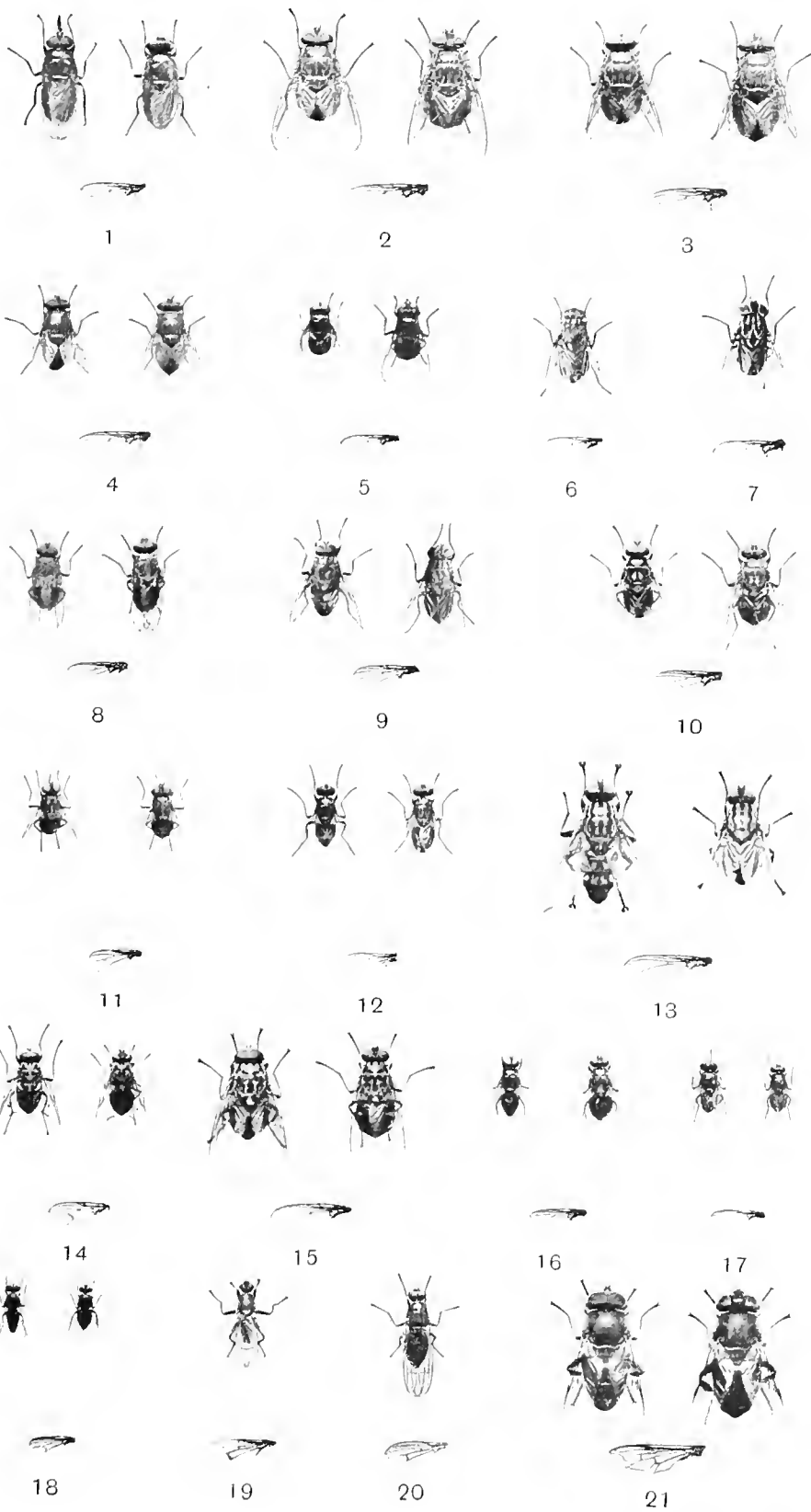
In rapidly identifying large numbers of flies mistakes are unavoidable, but the figures given in Table III fairly represent the distribution of the common species which were caught in these traps throughout the season. Under the heading of small *Anthomyidae* certain small flies not belonging to that family are probably included. The more uncommon species of larger flies, which only occurred in very small numbers, are omitted except in trap I. The very small species, capable of getting through the mesh of the net, have not been taken into consideration.

During the season 105,373 flies were caught in traps baited with excrement and animal matter. Traps in the open baited with excrement (39.5 %) and decomposing animal matter (37.6 %) attracted almost equal numbers. Dark receptacles in open situations caught smaller numbers (excrement, 10.6 %; animal matter 5.9 %), while traps in shady places attracted few flies (excrement, 3.6 %; animal matter 2.4 %), a large proportion of them relatively unimportant *Anthomyids*.

In this country it is desirable therefore to place all receptacles for garbage, manure, and refuse in the most shady situations available so as to attract as few flies as possible.

Some interesting information may be obtained by studying the records from comparable traps, I and IV, II and V, and III and VI, baited respectively with human excrement and decaying animal matter.

Traps I (excrement) and IV (animal matter) in open situations. In April small numbers of freshly emerged flies were attracted to trap I, but none to trap IV, and in May when flies were emerging in large numbers six times as many visited trap I as visited trap IV. From June to October, except in August when larger numbers visited trap IV,





TRAP IV. Baited with small carcasses. In an open situation.

	April		May		June		July		Aug.		Sept.		Oct.		Nov		Total		
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
C. erythrocephala	0	0	29	145	169	314	204	420	519	1044	285	1171	302	2017	8	119	1516 (22·3 %)	5230	6746
C. vomitoria ...	0	0	1	18	51	151	43	157	287	546	102	558	38	614	0	13	522 (20·2 %)	2057	2579
P. groenlandica ...	0	0	0	1	5	11	1	8	9	21	3	4	1	1	0	0	19 (29·2 %)	46	65
Lucilia ...	0	0	3	33	77	1152	150	864	228	4409	35	2654	2	194	0	0	495 (5·5 %)	9306	9801
P. eriophthalma ...	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1
P. cornicina ...	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M. stabulans ...	0	0	0	12	30	480	23	172	73	287	12	59	1	4	0	0	139 (12·0 %)	1014	1153
M. pabulumum ...	0	0	0	3	42	59	19	21	22	37	10	39	4	10	0	0	97 (36·4 %)	169	266
M. hortorum ...	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	3	3
Sarcophaga ...	0	0	8	10	26	49	5	24	15	22	8	23	0	2	0	0	62 (32·3 %)	130	192
O. cognata ...	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. dentipes ...	0	0	10	165	412	1856	760	1686	834	2725	334	2759	57	795	0	3	2407 (19·4 %)	9989	12396
P. lardaria ...	0	0	0	0	3	3	0	0	0	0	0	0	0	0	0	0	3 (50·0 %)	3	6
P. albolineata ...	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
O. leucostoma ...	0	0	0	3	166	886	29	388	470	2454	19	685	0	17	0	0	684 (15·0 %)	4433	5117
Scatophaga ...	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Small Anthomyidae	0	0	1	111	30	638	17	285	17	249	7	89	1	24	0	0	73 (4·9 %)	1396	1469
Total	0	0	52	501	1011	5599	1251	4025	2475	11797	815	8041	406	3678	8	135	6018 (15·3 %)	33776	39794

TRAP II. *Baited with excrement. In a shady situation.*

	April		May		June		July		Aug.		Sept.		Oct.		Nov.		Total	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
<i>C. erythrocephala</i>	0	0	10	31	74	132	41	131	27	87	34	121	3	35	0	0	189 (26 %)	537 726
<i>C. vomitoria</i> ...	0	1	1	4	29	39	33	52	15	14	10	29	0	0	0	0	88 (38 %)	139 227
<i>P. groenlandica</i> ...	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lucilia</i> ...	0	0	1	4	8	46	14	22	1	4	0	1	0	0	0	0	24 (24 %)	77 101
<i>P. eriophthalma</i> ...	0	0	0	2	0	4	2	0	0	0	0	0	0	0	0	0	2 (25 %)	6 8
<i>P. cornicina</i> ...	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>M. stabulans</i> ...	0	0	0	0	4	65	4	52	5	18	0	3	0	0	0	0	13 (9 %)	138 151
<i>M. pabulorum</i> ...	0	0	0	0	0	3	1	1	0	3	1	7	0	1	0	0	2 (12 %)	15 17
<i>M. hortorum</i> ...	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	3 3
<i>Sarcophaga</i> ...	0	0	0	0	2	9	1	14	1	17	0	0	0	0	0	0	4 (9 %)	40 44
<i>O. cognata</i> ...	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. dentipes</i> ...	0	0	6	32	35	292	59	287	20	70	3	78	0	3	0	0	123 (14 %)	762 885
<i>P. lardaria</i> ...	0	0	0	0	18	21	0	0	0	0	0	3	0	9	0	0	18 (35 %)	33 51
<i>P. albolineata</i> ...	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>O. leucostoma</i> ...	0	0	0	0	0	2	0	3	0	1	0	0	0	0	0	0	0	6 6
<i>Scatophaga</i> ...	0	0	11	14	1	5	6	4	3	3	2	1	19	77	0	2	42 (28 %)	106 148
Small <i>Anthomyidae</i>	0	4	5	156	39	777	12	248	12	192	0	49	0	0	0	0	68 (4 %)	1426 1494
Total	0	5	34	243	210	1396	173	815	84	410	50	292	22	125	0	2	573 (15 %)	3288 3861

TRAP VI. *Baited with small carcasses. Dark receptacle in open situation.*

	April		May		June		July		Aug.		Sept.		Oct.		Nov.		Total	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
<i>C. erythrocephala</i>	0	0	1	6	5	53	2	80	1	22	2	109	26	646	7	185	45 (3.8 %)	1128
<i>C. vomitoria</i> ...	0	0	0	1	2	16	0	42	1	15	0	44	1	298	0	29	4 (0.8 %)	445
<i>P. groenlandica</i> ...	0	0	0	0	0	2	1	2	1	0	0	1	2	1	0	0	4 (40 %)	6
<i>Lucilia</i> ...	0	0	0	8	1	271	0	544	0	276	0	611	0	86	0	0	1 (0.05 %)	1796
<i>P. eriophthalma</i> ...	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. cornicina</i> ...	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>M. stabulans</i> ...	0	0	0	12	2	57	6	43	9	25	0	16	1	5	0	0	18 (10.2 %)	158
<i>M. pabulorum</i> ...	0	0	0	0	4	16	4	16	3	7	1	8	0	12	0	0	12 (16.9 %)	59
<i>M. hortorum</i> ...	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sarcophaga</i> ...	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0
<i>O. eognata</i> ...	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. dentipes</i> ...	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. lardaria</i> ...	0	0	0	0	1	0	0	0	0	0	1	10	0	136	0	3	22 (6.4 %)	321
<i>P. albolineata</i> ...	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2
<i>O. leucostoma</i> ...	0	0	0	0	28	308	8	222	108	669	30	208	2	52	0	0	176 (10.7 %)	1459
<i>Scatophaga</i> ...	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Small Anthomyiidae</i>	0	0	0	37	0	165	7	202	1	113	0	22	0	97	0	0	8 (1.2 %)	636
Total	0	0	1	64	43	918	44	1269	129	1163	34	1029	32	1333	7	218	291 (4.6 %)	6021
																		6312

the two traps were equally attractive. In November trap IV became the most attractive.

Traps II (excrement) and V (animal matter) in shady situations. These two traps were in similar situations, but whereas trap II was an open net trap, trap V was a dark receptacle, and therefore less likely to attract flies. Up to July trap II was the most attractive, but in August, October and November more flies visited trap V.

Traps III (excrement) and VI (animal matter) both dark receptacles in open situations. Up to September trap III, which was protected from winds and the afternoon sun, was the most attractive, great numbers occasionally visiting it on very hot and windy days (p. 499), but in October and November a change occurred, large numbers of flies visiting trap VI, and none going to trap III. This was probably due to the fact that trap VI was more influenced by the heat of the sun than trap III. Moreover a large proportion of the flies caught during these months were old blow-flies attracted to animal matter in order to lay their eggs.

It would appear from these observations that early in the season when flies are emerging excrement is more attractive than decomposing animal matter¹, but late in the season, when recently emerged specimens are less common, animal remains are the more attractive, especially to the numerous females ready to deposit eggs.

Several experiments were made in order to ascertain how long masses of excrement retained their attraction for flies, traps being placed over fresh masses, and the flies caught and examined daily. In sunny places the attractive power was greatest on the first day, slightly less on the second, and was much diminished on the third. Flies in small numbers continued to be attracted up to the seventh day in some experiments. In the shade flies were seldom attracted after the third day.

That relatively fresh carcases are extremely attractive to flies of the genus *Lucilia* is shown by the following observation. The lacrated body of a recently killed bird was found covered with green-bottles in a country lane. The carcase was carried several hundred yards and then placed on the ground. Within a few minutes it was again covered with these flies although none of them were seen to be following.

¹ Between April 21 and May 2, 1916, 1294 flies, 462 ♂ and 832 ♀, visited a trap baited with excrement, and only 11 flies a trap baited with small carcases. Towards the end of May the latter trap became more attractive.

Species of flies caught in traps.

Most of the species enumerated in Table III seldom enter houses, and under ordinary conditions in this country are of little importance as disseminators of disease-producing bacteria. Several of them, however, play an important part in spreading disease and causing discomfort under war conditions¹. In this category may be included *C. erythrocephala*, *C. vomitoria*, *Lucilia*, *M. stabulans*, *Sarcophaga*, *H. dentipes*, *O. leucostoma* and the small *Anthomyidae*, all of which visit in large numbers both excrement and decaying animal matter. On the other hand several of the numerically less important species, including *P. eriophthalma*, *P. cornicina*, *M. hortorum*, *P. lardaria* and *Scatophaga*, frequent excrement, but seldom visit animal matter.

In this country shade seems to be specially repellent to *P. groenlandica*, *P. cornicina*, *M. hortorum* and *O. leucostoma*, and members of some other species belonging to the genera *Calliphora*, *Lucilia*, *Muscina*, *Sarcophaga*, *Hydrotaea* and *Polictes* are seldom found in shady places. On the other hand *A. radicum* and other small *Anthomyidae* are usually abundant in shady places. As very intense heat appears to be harmful to flies this statement is possibly incorrect for certain seasons in the tropics.

Sexes of flies caught in traps.

Reference to Table III will show that of the flies which visited these traps only 16,624 (16 %) were males, though specimens of this sex were often attracted to the neighbourhood of the traps. Males were caught relatively more commonly in the open traps. They very seldom ventured into the dark receptacles, especially those containing animal remains, where the proportion of females was as high as 95 %, or, if the males of *O. leucostoma* be excluded, 98 %.

In regard to the important species *C. erythrocephala*, *C. vomitoria* and *Lucilia* it may be stated that the males prefer excrement and avoid dark and shady places, whereas the females will venture into dark receptacles, especially if situated in sunny places, in order to deposit their eggs. Certain observations seem to indicate that both sexes of these species mainly visit excrement exposed in the open in order to feed on it. The excrement from trap I was removed frequently and

¹ Atkinson, E. L. (iv. 1916) found *M. domestica*, *F. canicularis*, *F. scalaris*, *C. vomitoria*, *C. erythrocephala*, *L. caesar*, *S. carnaria*, *M. stabulans*, and "a stout hairy fly almost black in colour" the most prevalent flies in Gallipoli.

placed in earthenware pipes half buried vertically in the soil. From these pipes very few flies emerged and neither eggs nor larvae were often noticed in this material, though both eggs and larvae of many species were usually present in large numbers in excrement from the shade trap II.

Ages of flies visiting the various baits.

Some direct evidence as to the age of the flies of the genus *Lucilia* visiting excrement and animal matter was obtained. All flies captured belonging to this genus were pinned, and it was early noticed that some were so newly emerged and soft that the chitin of the thorax gave way before the pin, rendering it almost impossible to obtain satisfactorily mounted specimens. In others the chitin was harder, and in many old specimens very hard. During part of July careful daily notes were kept as to the condition of the 1081 flies of the genus *Lucilia* caught in traps I, IV and VI. The very soft flies were recorded separately from the moderately hard and hard specimens. During this period 130 females, all hard, but no males visited the dark trap in the open baited with animal matter (VI). The open trap baited with animal matter (IV) was visited by 302 flies, 88 males and 214 females, of which 88 (29 %) were soft, young specimens. Of the males 36 (41 %) were soft and of the females 52 (24 %). The open trap baited with excrement (I) was visited by 649 flies, 298 males and 351 females, of which 433 (66 %) were soft. Of the males 235 (78 %) and of the females 198 (56 %) were soft.

It is evident, therefore, that the very young specimens of both sexes are mainly attracted to excrement as a food, since of the 521 young flies caught 433 or 83 % visited traps baited with excrement and only 88 or 17 % traps baited with decaying animal matter. At this period of the year the older specimens visit excrement and animal remains in the open in equal numbers, but old females only are attracted to decaying animal matter in dark receptacles.

Judging from the scattered observations which were made in regard to blow-flies the same rule seems to apply to them.

Flies visiting fruit.

All the species of flies which visit excrement and decaying animal matter also visit ripe fruit in the late summer and autumn months, but not in the same proportions either as regards species or sexes. The most common species visiting fruit are *C. erythrocephala*, *M.*

stabulans, *Sarcophaga*, *Lucilia*, *C. vomitoria*, *M. pabulorum*, *Mydaea* and small *Anthomyidae*. Other species are found more rarely, the small numbers of *H. dentipes* and *O. leucostoma* attracted to fruit being specially remarkable.

TABLE IV.

TRAP VII. *Baited with fruit. In an open situation.*

	Aug.		Sept.		Oct.		Nov.		Total			
	♂	♀	♂	♀	♂	♀	♂	♀	♂			♀
<i>C. erythrocephala</i>	22	41	95	140	148	146	55	61	320 (45.2 %)	388	708	
<i>C. vomitoria</i> ...	10	7	17	12	22	27	0	1	49 (51.0 %)	47	96	
<i>P. groenlandica</i> ...	0	1	0	1	0	0	0	0	0	2	2	
<i>Lucilia</i> ...	15	45	12	30	3	4	0	0	30 (27.5 %)	79	109	
<i>P. eriophthalma</i> ...	0	0	0	0	0	1	0	0	0	1	1	
<i>P. cornicina</i> ...	0	0	0	0	0	1	0	0	0	1	1	
<i>M. domestica</i> ...	0	1	0	2	3	2	0	0	3 (60.0 %)	5	8	
<i>M. stabulans</i> ...	39	108	28	56	6	22	0	0	73 (28.1 %)	186	259	
<i>M. pabulorum</i> ...	9	16	11	17	13	19	0	0	33 (38.8 %)	52	85	
<i>P. rudis</i> ...	0	0	3	5	2	1	0	1	5 (71.4 %)	7	12	
<i>Sarcophaga</i> ...	37	33	32	31	5	9	0	0	74 (50.3 %)	73	147	
<i>Mydaea</i> ...	1	2	0	39	3	20	0	3	4 (0.5 %)	64	68	
<i>H. dentipes</i> ...	0	0	0	5	0	7	0	2	0	14	14	
<i>P. lardaria</i> ...	0	0	0	0	1	2	0	0	1	2	3	
<i>O. leucostoma</i> ...	0	2	0	0	0	0	0	0	0	2	2	
<i>Scatophaga</i> ...	0	0	0	0	0	0	1	3	1	3	4	
Small <i>Anthomyidae</i>	6	16	4	11	8	15	0	1	18 (29.5 %)	43	61	
Other flies ...	2	5	3	4	5	4	0	2	10 (24.0 %)	15	25	
Total	141	277	205	353	219	280	56	74	621 (38.7 %)	984	1605	

In the trap baited with ripe fruit the males of most species were caught abundantly, forming 38 % of all the flies captured. They were also very common on fruit hanging on trees, being sometimes found in considerable numbers on plums on stormy days when very few females were about.

A few experiments with plums were made in August in order to ascertain roughly the extent of contamination caused by flies and wasps. Ripe plums from two gardens were removed from the trees with sterile forceps, and dropped separately into sterile, wide mouthed bottles. Three plums which were apparently perfect were washed with sterile salt solution, and cultures prepared from the fluid on agar and on McConkey's lactose-bile-salt-neutral-red medium. Only a few unimportant organisms, spore producing bacilli, cocci, etc., grew in these cultures. Seven plums were chosen in which wasps and other creatures had gnawed holes. Sterile salt solution was poured into these cavities

and stirred with a sterile platinum needle, and cultures made on the media mentioned with two loopfuls of the fluid. Two plums with small holes yielded amongst other organisms a few colonies of *B. coli*. Four with large cavities yielded numerous colonies of *B. coli*, but one with a large hole yielded no faecal bacteria.

It may be inferred from these few experiments and from the known habits of flies and wasps (p. 504) that great contamination of fruit hanging on trees and exposed for sale with faecal and putrefactive bacteria must be caused by these and other insects.

Outdoor habits of Musca domestica.

One of the most remarkable features of these experiments is that amongst the 106,978 flies caught in various traps only ten specimens of *M. domestica* occurred, two in trap VI, and eight in the trap baited with fruit (VII). This was not due to the absence of this species, for hundreds entered the house and examples were not infrequently seen and caught in various parts of the garden. Moreover specimens were very seldom seen on the carcasses of large or small animals, exposed in various other places.

THE INFLUENCE OF WEATHER ON FLIES.

No attempt appears to have been made hitherto to study the effects of different weather conditions on the habits of flies. Throughout the year 1915 careful notes were kept of the daily weather conditions and records were obtained of the velocity of the wind, of the rainfall occurring in the daytime and at night, of the hours of bright sunshine, and of the readings of thermometers placed in various situations. These meteorological data have been studied in conjunction with the records of flies caught in various traps, and observations on "wild" flies in the garden.

Unfortunately after June the season of 1915 was abnormally cold, the mean temperature in the screen in July being 2.5° F., in August 1.3° F., in September 1.4° F. and in November 3.8° F. below the average. July and August were also unusually wet.

The more important meteorological conditions affecting flies are first discussed, and then the combinations of these conditions which make up different classes of days.

Bright sunshine. In meteorological records it is the practice to quote only the number of hours of bright sunshine per week. Such statements are of little value in considering the effects of weather on

flies, since these insects are seldom active before 8 a.m. and do not appear to be influenced by the early hours of sunshine. Nor are they usually active after 6 p.m. In this country, therefore, only the influence of bright sunshine occurring between 8 a.m. and 6 p.m. need be considered.

Undoubtedly flies tend to be most active in bright sunshine, though on bright days with cold winds they often only emerge from their retreats to sun themselves in sheltered situations. They also seem to avoid very hot sunshine, for during the hottest hours of exceptionally hot days very few flies are caught in traps or enter rooms, and many of those confined in exposed traps die.

Many days occur in the spring and autumn and a few in summer on which flies are active only during brief intervals of bright sunshine.

Cloudy days. In May, October and November flies are usually very inactive on dull cloudy days, but during the rest of the season they are moderately active on such days, if the temperature is not too low.

Wind. Flies appear to be extremely sensitive to wind, and on very windy days, whether hot or cold, seldom venture into the open, though they may be moderately active and abundant in sheltered situations. Days with very little wind and otherwise suitable are the most favourable.

Rain. Flies seldom venture out of their hiding places in rain, fog, or mist, but are often very abundant between heavy showers on warm days.

Temperature. The activities of flies are more influenced by temperature than by any of the weather conditions yet mentioned. When the temperature is low they are very inactive, and seldom make any attempt to move, and on the other hand when the temperature is very high they seem to suffer from the heat.

A number of charts were constructed on which the daily numbers of flies caught in traps, the hours of bright sunshine and of rainfall between 8 a.m. and 6 p.m., the mean velocity of the wind, the maximum temperatures recorded by thermometers exposed to the sun and in the screen, the minimum temperatures recorded by thermometers in the screen and on the grass, and the mean temperature in the screen were plotted. These charts showed that the curve for flies caught in traps corresponded most closely to the curve for the maximum temperature recorded by a thermometer exposed to the sun (Chart 5).

On a few occasions the flies caught in the traps were counted hourly, and the results obtained on June 12, a very fine day, are illustrated in

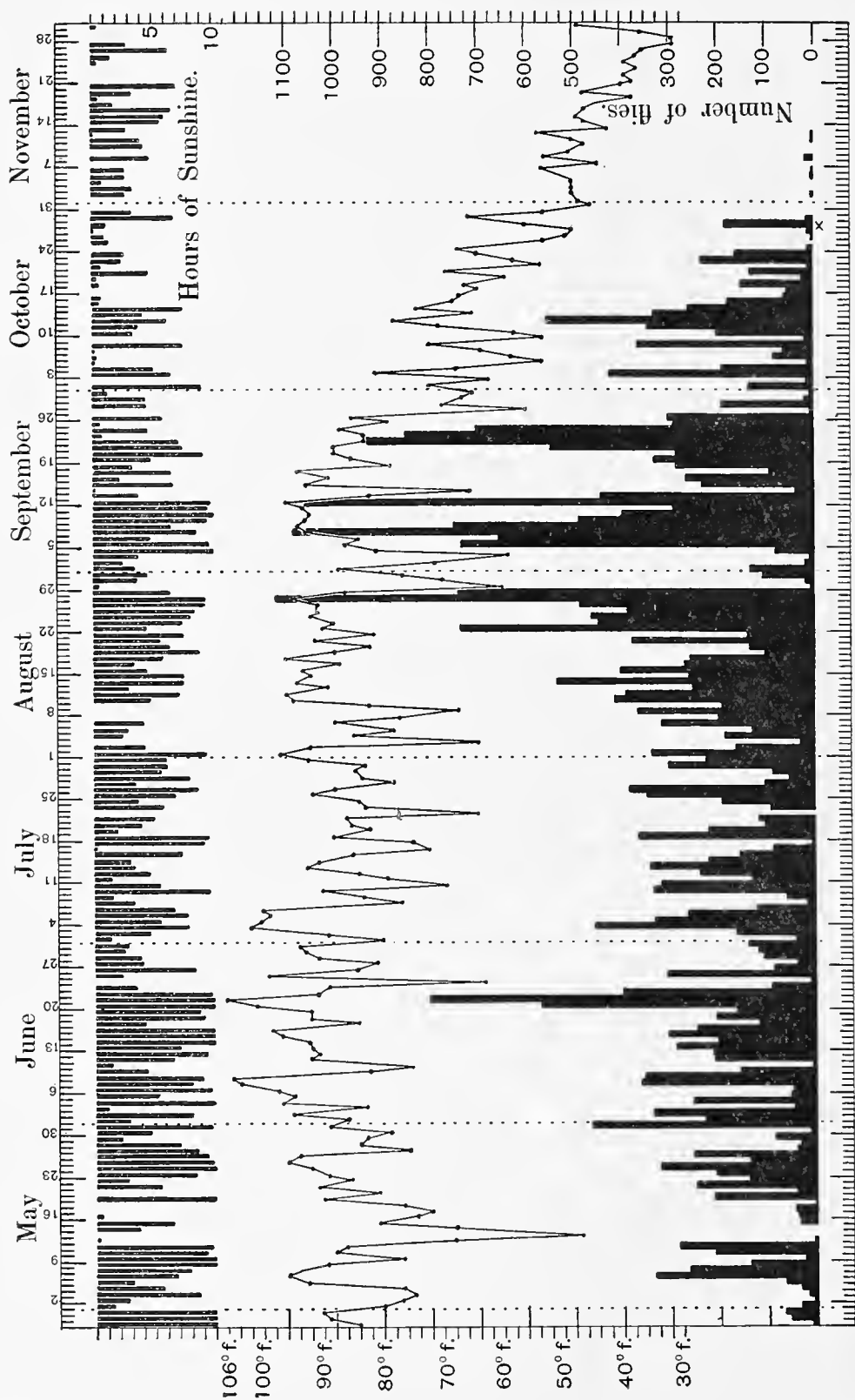


Chart 5. Showing the daily hours of bright sunshine between 8 a.m. and 6 p.m. (columns at the top of the chart), the maximum temperature recorded daily by a thermometer exposed to the sun and the numbers of flies caught daily in a trap in the open baited with human excrement (Trap I). The column marked x should represent the flies caught on October 29.

Chart 6. It will be noticed that the numbers gradually increased up to 1.30 p.m., after which there was a rapid fall to a moderate level, and then a gradual decline. The curve for flies on such days corresponds closely in form to the curve for the hourly readings of the "sun" thermometer. The influence of the sun temperature on the activities of flies could be investigated most satisfactorily with the aid of a thermograph placed in the neighbourhood of the traps.

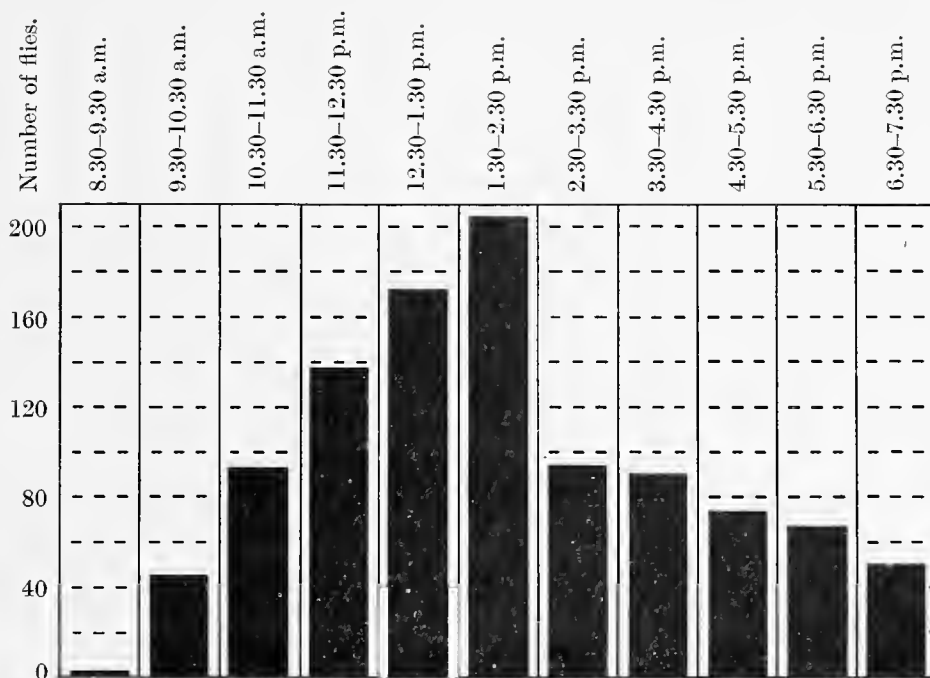


Chart 6. Showing the number of flies caught hourly in the various traps on June 12, 1915.

Oppressive, sultry days. A remarkable and interesting effect of weather conditions on flies was noticed on a few occasions. September 15 and 16 were very sultry, oppressive days, and the blow-flies in the outdoor cage were greatly affected. They were disinclined to fly, crawled about slowly, clung tenaciously to the clothes of persons entering the cage, and died in large numbers (p. 464). "Wild" flies seemed to be similarly affected. Very unusual numbers visited trap III, a dark receptacle baited with excrement, which was in the shade in the afternoon; many of those caught in the traps died, and very few entered the house except in the morning and evening. June 7 and 8 and July 5 and 6 were somewhat similar days, and produced identical,

though less marked, effects on flies. The phenomenon is common in hot seasons, and people speak of the flies being "sticky."

Flies are most abundant and active on days with several hours of bright sunshine after 8 a.m., very little wind, and the "sun" thermometer reaching between 90° F.–100° F. On such days throughout the season of 1915 the largest numbers were attracted to traps, and large numbers were seen flying from flower to flower, and settling on palings, etc. Very sunny days on which the sun temperature is higher, and the shade temperature unusually high, are not very suitable as the flies are lethargic during the hottest hours. On sunny, warm but windy days flies may be attracted in moderate numbers to traps, but they do not resort to flowers, or settle on palings. Very strong north or north-east winds cause almost all activity to cease even on sunny days. On bright frosty days in autumn flies leave their shelters to bask in the sun.

Flies are moderately active on warm days with little sunshine, and no wind throughout the summer, but such days do not suit them in April, May, October or November.

Flies are lethargic and "sticky," visit sheltered places and die in large numbers on very hot, windy, oppressive days with or without sunshine.

Flies seldom leave their retreats on rainy, damp, foggy, cold, or very windy days. On poor fly days males are relatively much more active than females.

Chart 7 shows the effects of varying weather conditions on the numbers of flies caught in the traps during the season of 1915.

OUTDOOR HABITS OF FLIES.

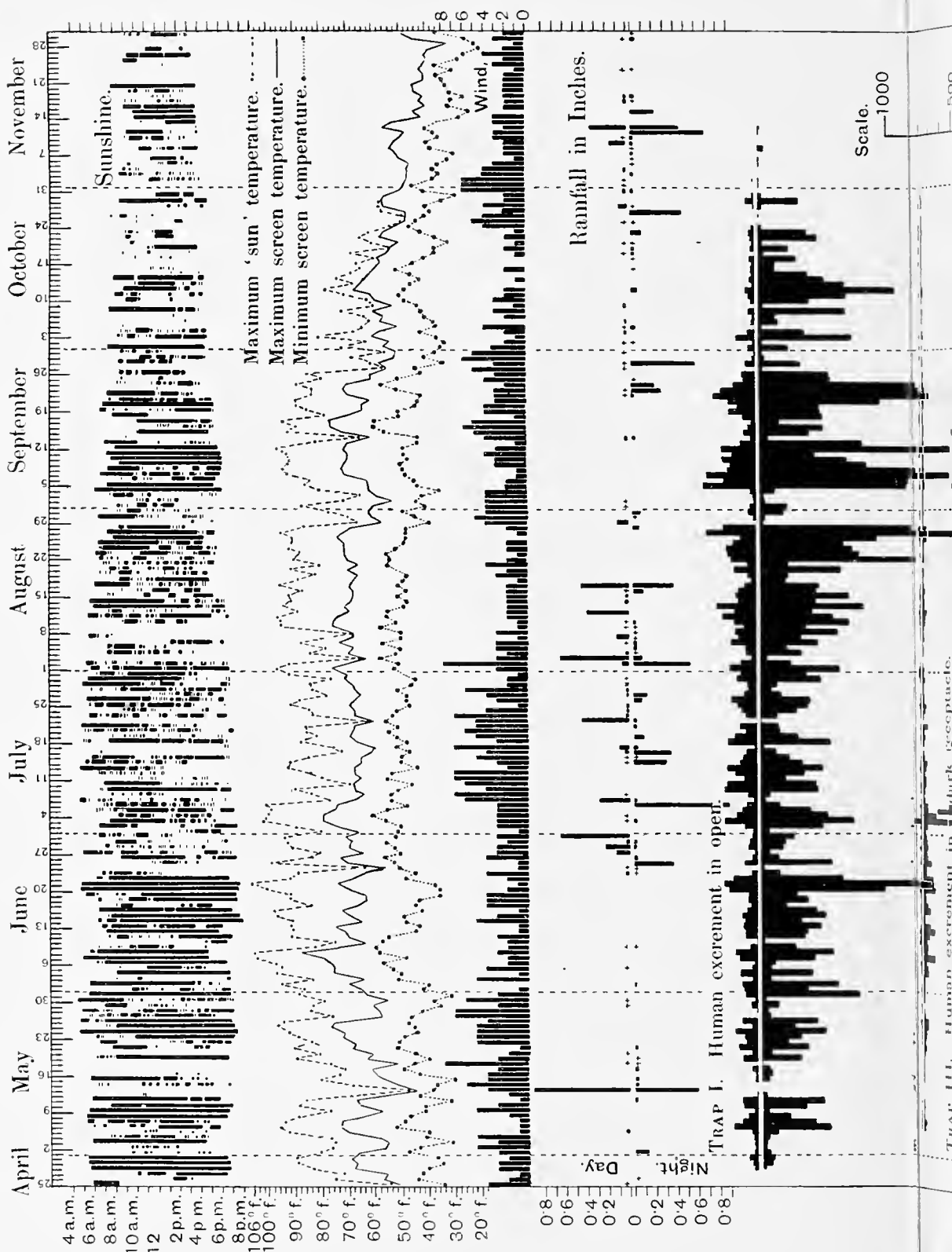
(a) *Blow-flies confined in an outdoor cage.*

The breeding experiment previously described (p. 458) afforded excellent opportunities for studying the outdoor habits of blow-flies, and an endeavour was made at the same time by observing "wild" flies to ascertain whether they responded to varying conditions in the same ways.

Even in the finest and warmest weather the blow-flies in the cage did not begin to move about freely much before 8.30 a.m. On the other hand flies usually emerge from pupae rather earlier in the morning (p. 451).

On sunny days the blow-flies were very active, continually flying





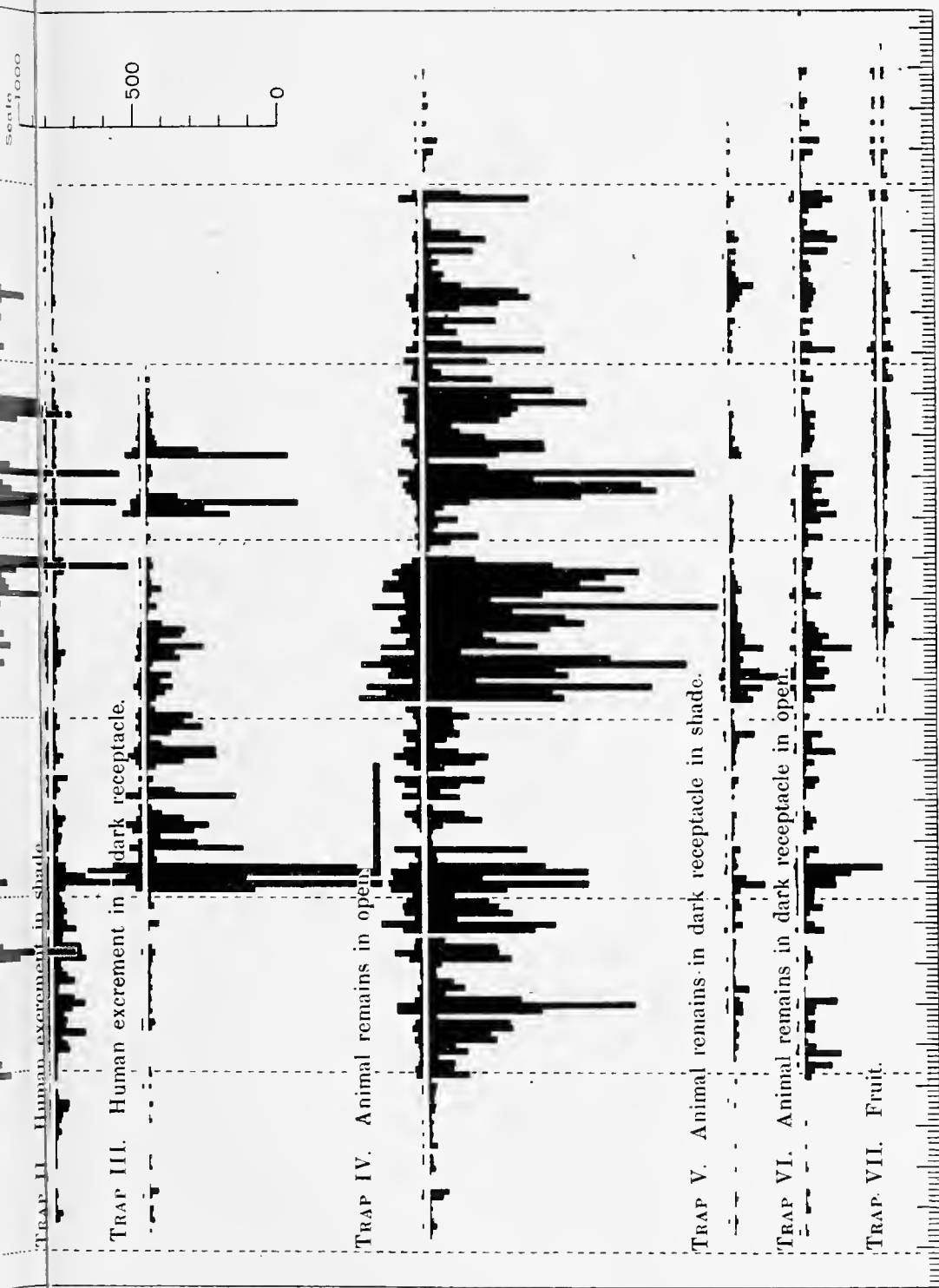


Chart 7. Illustrating the effects of weather on flies. The chart shows the daily periods of bright sunshine, the daily maximum temperatures recorded by thermometers exposed to the sun and in the screen, the daily minimum temperature in the screen, the approximate velocity of the wind in miles per hour during the day time, and the rainfall during the day and night. The numbers of flies, males above and females below, caught daily in each of the seven traps are indicated by columns.



about, and, except when feeding, seldom remaining long in one place. This occurred even when the day was moderately cold. Very close, sultry weather had a peculiar effect. The flies became very sluggish, were apparently unwilling or unable to fly, and clung tenaciously to anything on which they settled. Such weather caused great mortality. Their behaviour on overcast days with brief periods of sunshine was most interesting to watch. When the sun came out flies, which were taking refuge in crevices, began to stir, and soon came out into the sunshine. If the day was warm they flew about, but if it was cold they remained close to the crevices, and when clouds obscured the sun often went back slowly into their sheltering places. On cold days with gleams of sunshine the flies were often seen sunning themselves in a peculiar manner. They so arranged themselves as to present their dorsal surfaces as much as possible to the sun, often leaning at considerable angles in order to accomplish this, with the legs of the side nearest to the sun contracted and those of the opposite side more extended. On sunless days the flies seldom flew, and usually remained very quiet, occasionally walking slowly from place to place. In very cold weather they remained motionless in crevices and corners for days together.

In windy weather the flies moved about very little, but sought situations sheltered from the wind.

During rain the flies usually congregated in protected situations, and changed the situations first chosen, if the direction of the rain altered.

The behaviour of the flies in the evening depended on the temperature. On warm evenings they were widely distributed near the roof of the cage and did not go into corners, etc., but on cold evenings they gathered in clusters in the corners, often close to the ground (Pl. XXIII, fig. 28), and many sought shelter in crevices.

As the flies often clustered in large numbers in dark corners and were in consequence difficult to count, white strips of wood were fixed in these corners to render counting easier, but after this most of the flies avoided these white pieces of wood, and seemed to prefer to settle, especially in the evening, in darker places, where they were less visible. This hypothesis seems to be confirmed by the fact that the under surfaces of dark, dead artichoke leaves, where the flies were almost invisible, were very favourite resting places in the evening.

Flies depositing eggs and feeding on animal carcasses often seem to be so occupied that they are not easily disturbed, and on cold or sunless days many will not move, even if touched. For oviposition they seem

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to prefer surfaces almost in contact with the ground, natural openings, such as the mouth, nose and ears, or wounds.

Occasionally they were seen feeding in great numbers on old artichokes, which had been turned up from the ground.

For some considerable time before settling down for the night nearly every fly is occupied in "blowing bubbles," repeatedly regurgitating a large drop of fluid, and sucking it back again. This procedure is less commonly seen at other times of the day.

(b) "*Wild*" flies.

Wild flies behave very similarly. They are seldom active before 8.30 a.m. and are most active on sunny days. On cold autumn days with sunny intervals they were seen to emerge from crevices and sun themselves (Pl. XXIII, figs. 29, 30), and in oppressive weather they behaved in unusual ways. Specimens were seen "blowing bubbles" almost daily.

It is evident, therefore, that much, otherwise difficult to ascertain, may be learnt about the habits of "wild" flies by observing the behaviour of captive flies in large cages out of doors.

It is impossible, however, to study some of their habits in cages. On warm sunny days with little or no wind many species settle on certain flowers, but seldom resort to flowers on very hot, dull or windy days. When flies are emerging in large numbers very soft, young specimens are common on flowers. In the spring hawthorn flowers are a great attraction to many species. On the approach of an observer specimens of many species sitting on flowers, palings, walls and other situations crouch closer and approximate their wings more closely together, apparently with the intention of making themselves less visible and escaping detection.

Flies belonging to the genus *Lucilia* and *O. leucostoma* seem to be peculiarly active in sunshine, and are seldom seen in large numbers except on warm sunny days. The males of *O. leucostoma* hover in the air like some of the *Syrphidae*.

THE LARVAE OF COMMON FLIES.

A considerable number of observations were made on the habits of the larvae of some of the common species, but as it is proposed to carry on further investigations during the coming season only certain observations of special interest will be recorded.

In many species the tendency to migrate, especially in wet weather, is very marked, even when the food supply is abundant, and special

provisions to prevent migration have to be made, if any conclusions are to be drawn as to the numbers of flies developing from various masses of food. The tendency to migrate is most marked in the older larvae, but even very small ones migrate under certain conditions.

The eggs are generally laid under the edges of pieces of meat, on the hair of animal bodies close to the ground or in the mouth, nose, ears or anus. Maggots usually feed under the skin or in the interior of carcasses, but live freely on the surface, if the food is in darkness, and disappear into the depths with remarkable rapidity when it is exposed to the light.

According to the observations of Portchinsky (1913) and of Keilin (1915) the larvae of several of the common species of flies feed on the larvae of other species. Placed in order of the abundance of the adults the most important carnivorous larvae are those of *Hydrotaea dentipes*, *Muscina stabulans*, *Graphomyia maculata*, *Poliates albolineata*, *Phaonia erratica* and *Azeria macquarti*.

The enormous destruction of the larvae of common flies wrought by the larvae of *H. dentipes* alone has not been taken into account hitherto. Such carnivorous larvae must be extremely important natural agents in limiting the numbers of many of the species likely to carry pathogenic and putrefactive bacteria to human food.

On July 7 a large piece of sheep's lung containing some eggs and very small larvae was buried to a depth of $1\frac{1}{2}$ feet, and the earth well packed down. The earth was further trodden down on July 9. On July 12 the material was exhumed and numerous large, apparently healthy larvae were found in it.

Later a series of similar experiments were carried out to ascertain the effects of burial on larvae.

On September 4 the bodies of six guinea-pigs were exposed. On the same day one of the carcasses with eggs in the mouth and on the hair was buried to a depth of a foot in an earthenware pipe sunk vertically in the ground. A little earth was placed above the carcass and packed down tightly, and the process repeated till the pipe was full. The top of the pipe was sealed with an earthenware saucer. The other carcasses containing larvae of various sizes were similarly buried on September 8, 10, 11 and 14. On September 26 large full fed larvae and pupae were noticed just below and on the surface of the earth in all the pipes. Blow-flies began to emerge simultaneously from all the pipes on October 17, and large numbers were caught up to October 29, and smaller numbers up to November 15.

These observations show that larvae emerge from eggs and thrive

in buried carcasses, and moreover that they are little, if at all, retarded in their development, since flies emerge at the same time from carcasses buried while eggs only are present on them, and from half-eaten carcasses containing large larvae. Further the larvae are able to make their way up through tightly packed earth to the neighbourhood of the surface, where they pupate. The burial of a carcase therefore does not prevent flies emerging from the eggs already laid, and only limits the production of flies by preventing later batches of eggs from being deposited.

To illustrate the number of flies which may emerge from a carcase the following experiment may be quoted. The body of a medium sized guinea-pig was exposed for thirteen days, and then placed in an earthenware pipe and lightly covered with earth. Fourteen days later flies began to emerge. Altogether 2511 flies appeared, 1122 male and 1059 female *Lucilia*, 182 male and 145 female *C. erythrocephala*, and 3 *O. leucostoma*, some of which were normal in size, and others small, indicating that the food supply was not quite sufficient.

It is probable that under natural conditions large numbers of larvae, which feed on animal matter, perish from lack of food. Numerous eggs were often noticed on the bodies of very young birds fallen from nests. Such bodies could only afford food for a very limited number of larvae.

Larvae which do not die of hunger, but are underfed, produce small flies (see Graham-Smith, 1914, Plates xxv, xxvi). According to Griffith (1908) small specimens of *M. domestica* are sterile, but this is not the case in *C. erythrocephala*. The writer confined several newly emerged very small blow-flies of both sexes in a cage, and eggs were deposited from which blow-flies of normal dimensions were reared.

WASPS.

Up to the present no one seems to have pointed out that wasps, owing to their filthy habits, may be the carriers of pathogenic and putrefactive bacteria to articles of food.

Wasps of the common species, *V. vulgaris*, *V. sylvestris* and *V. germanica*, were caught in traps placed over human excrement. Whether they were attracted to this material in order to feed on it, or to hunt the flies, which resort to it, is not quite clear, but contamination of their feet and jaws with such material was frequently noticed.

They are also greatly attracted to decaying animal matter in all stages of decomposition. In carrying out investigations on the putrefaction of animal carcasses, and the means of arresting the process, many bodies of large and small animals were exposed in an open field four

miles away. Wasps came to these carcasses in large numbers, occasionally in sufficient numbers to interfere with observation, and were seen feeding both on the flesh, when this was exposed, and on the fluids which escaped from the bodies. Under these conditions they must have become grossly contaminated with putrefactive and other bacteria. They also chased and frequently caught blow-flies, green-bottles and other flies, which came to the carcasses. After removing its wings the wasp generally flew away with the body of the fly. Since flies are invariably contaminated, the wasps which catch and devour them must also become contaminated. Traps placed over the carcasses of small animals caught them frequently.

A number of observations were made on plums hanging on trees, in order to ascertain the species of flies which came to them. In the course of these observations wasps were seen both to eat the fruit and to catch the flies feeding on it. Investigations on the bacterial contamination of plums have been quoted previously (p. 495). In regard to fruit, however, experiments carried out by placing over-ripe fruit under a trap (p. 494) on the ground were the most instructive. Very large numbers of wasps were caught, on some days exceeding the flies in number. When the wasps and the flies reached the balloon trap the former pursued the latter, especially the various species of the genus *Sarcophaga*, and tearing them to pieces devoured them.

Wasps also come into houses, especially into kitchens, in great numbers, and settle on all kinds of food.

It is evident from their habits that the legs and mouths of wasps and their excrement must usually be much contaminated, but whether they are capable also of causing infection by regurgitating their food is not clear.

These insects were more active than flies in cold, disagreeable weather, and were often caught in the traps, when few flies were about. It was noticed also that they were active earlier in the morning than flies.

During the season 150 wasps were caught in the traps baited with excrement, 79 in traps baited with animal matter, and 973 in traps baited with fruit. Of the 1202 wasps caught in traps, 951 appeared to be *V. germanica*, 123 *V. sylvestris* and 128 *V. vulgaris*.

Taking into consideration the extent to which they visit fruit, whether on trees or exposed for sale in shops, their well-known partiality for jam, sugar and other foods, and their liking for excrement, decaying animal matter and flies it seems very probable that they act not infrequently as agents in disseminating pathogenic and putrefactive bacteria.

EMPUSA DISEASE.

The mode of infection in this disease is at present not well understood, and the writer hopes that his observations and experiments may help to carry us a step further.

Brefeld (1873) successfully inoculated the spores of *Empusa muscae* under the skin and obtained germination of the gonidia on the surface of the fly.

Olive's (1906) experiments with an allied species, *E. sciara*, indicate that infection may occur in the very young larvae on the surface of excreta, before they burrow into its depths. Güssow (1913) infected flies by painting them with water containing spores, and he found also that he could infect flies by bringing them into contact with dead flies covered with spores. He suggests that "it is not unlikely that the fly becomes more susceptible to the disease as it grows older, while newly emerged broods are more or less resistant."

Hesse (1914) thinks that "the theory, expressed in published works, that the fungus, *E. muscae*, attacks the fly from the exterior does not seem very credible." He succeeded in infecting flies by allowing them to feed on empusa spores and also by allowing them to feed on spores derived from cultures made from flies dead of the disease. These cultures, it should be noted, produced a fungus identical with *M. racemosus*.

Bernstein (1914) also succeeded in infecting flies by the same means. He seems to think that the larvae may become infected, but says that "the question as to whether the disease can be transmitted from fly to fly in the adult stage is still unsettled, and experimentally it has not proved successful." Ramsbottom (1914) has up to the present failed to cultivate empusa from a single spore, and seems inclined to doubt whether the *Mucor*, which usually grows in cultures from infected flies, has any connection, as Hesse asserts, with *Empusa*.

Thaxter (1888) in America found *Empusa muscae* on several species of hover-flies (*Syrphidae*) and records its occurrence in *L. caesar* and *C. vomitoria*, and states that two other species of empusa, *E. sphaerosperma* and *E. Americana* occasionally attack house-flies and blow-flies. The former species destroys insects belonging to several orders. Lucas (1908) exhibited to the Entomological Society of London "a spike of the grass *Molinia caerulea* with dead Syrphids, *Melanostoma scalare* Fabr., attached by the parasitic fungus *Empusa muscae*, found on Esher Common, October 3, 1908. Most were attached by the point of



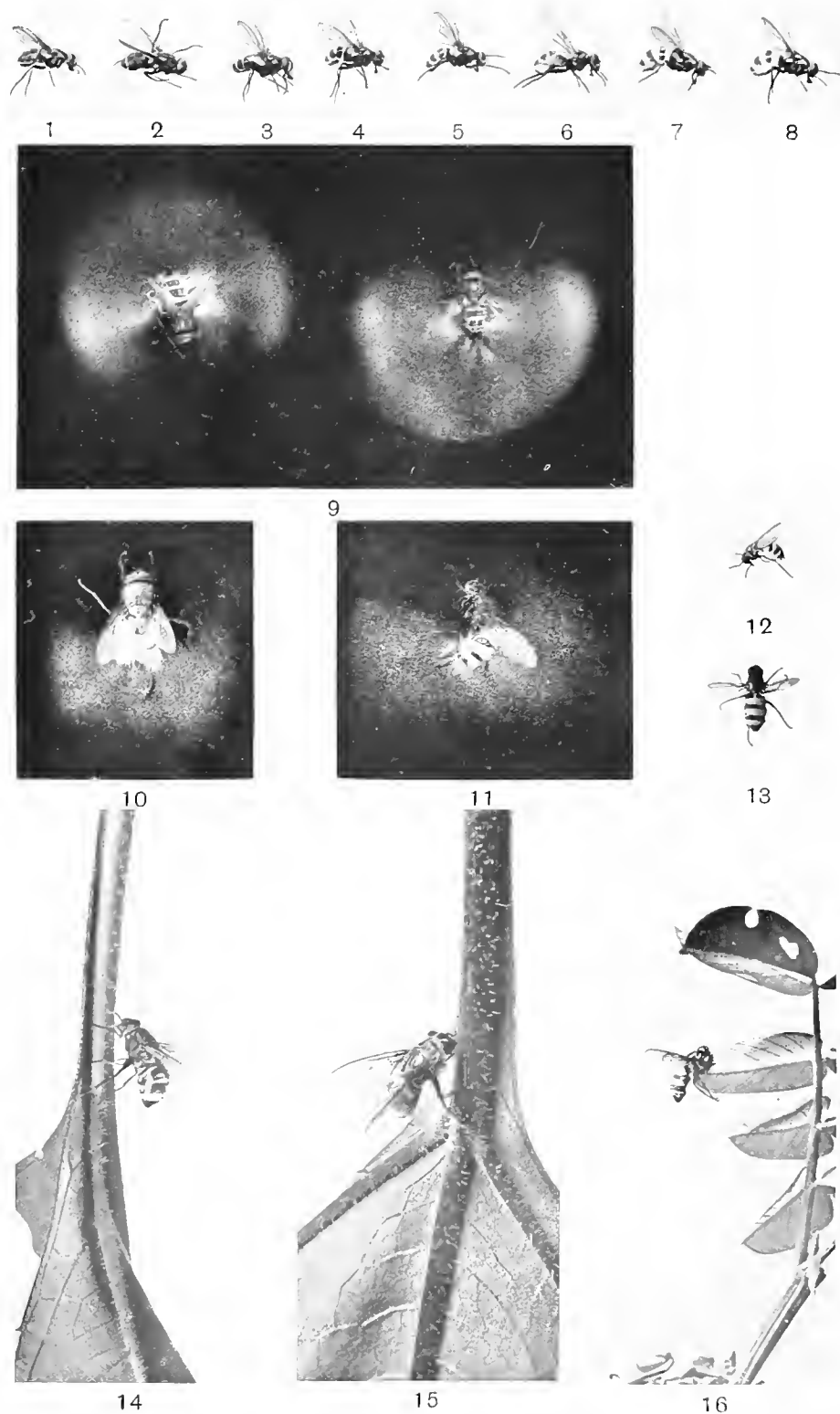


Plate XXVIII. Figs. 1-8. Photographs of specimens of *M. domestica* (nat. size) showing progressive signs of empusa disease. Fig. 9. Photographs of two empusa infected specimens of *M. domestica* (nat. size) with halos of spores. Figs. 10, 11. Photographs of empusa infected specimens of *C. erythrocephala* (nat. size) with halos of spores. Fig. 12. Photograph of a female *P. canicularis* (nat. size) suffering from empusa disease. Fig. 13. Photograph of a female *H. dentipes* (nat. size) suffering from empusa disease. Figs. 14, 15. Photographs of specimens of *C. erythrocephala* (nat. size), dead of empusa disease, attached to artichoke leaves. Spores may be seen on the leaf under the fly illustrated in Fig. 15. Fig. 16. Photograph of a female *H. dentipes* (nat. size), dead of empusa disease, attached to a leaf of *Galega*.

the head only in a very peculiar manner, and apparently all were females."

Nearly all investigators of this disease have confined their attention to house-flies observed in rooms, and do not seem to have taken into consideration the possibility of the disease occurring in other common flies, which are abundant earlier in the year, and the infection spreading from them to house-flies or their larvae, which frequent similar situations. In fact the cases just quoted seem to be the only ones recorded of flies, other than *M. domestica*, being attacked. Hewitt (1914) says that it is uncommon to find infected house-flies out of doors though he has observed some in Canada, at Ottawa.

Under out-of-door conditions an empusa-infected fly remains in a typical and easily recognisable condition for a short time only so that much patient labour would be required to ascertain whether the disease is common outside either among house-flies or other species.

The writer has found specimens of *Hydrotaea dentipes* dead of empusa out of doors on four occasions. The interest of this observation lies in the fact that this fly is very common and is attracted in large numbers to excrement and decaying animal matter, where it may come into contact with house-flies or their larvae. One was discovered on an artichoke leaf on August 4, 1914, and the others in 1915; one on August 16 on a *Galega* leaf (Plate XXVIII, fig. 16), a third on September 20 on an elm branch, and a fourth on October 4 on a piece of galvanised iron. In these years careful watch was kept for the occurrence of empusa disease in house-flies, and in each year an infected *H. dentipes* was found before the first infected house-fly was observed, the first case of empusa in the house-fly in 1915 being noticed on Aug. 30 in the kitchen.

Blow-flies (*C. erythrocephala*) become infected occasionally, but the growth on the abdomen is often less apparent than in house-flies. With careful observation, however, infected specimens may be found. In these insects the growth, in the early stages, appears as white, regular, wax-like bands between the abdominal segments. In well-marked cases the insect later resembles in every respect an infected house-fly. Plate XXVIII, figs. 10, 11, 14 and 15 reproduce photographs of specimens with well-marked rings of growth. The disease killed a number of the blow-flies bred from winter pupae and confined in an experimental cage (p. 458). The first case was noticed on Sept. 18 and the last on Nov. 12; during which period 18 cases of the disease occurred at considerable intervals. Approximately 0.33 % only of the blow-flies

became infected, and nothing resembling an epidemic developed. Although 309 blow-flies were still alive on Nov. 11, no further cases occurred amongst them. A female of *F. canicularis* showing marked infection with empusa was found in a room on Oct. 15 (Plate XXVIII, fig. 12), and another on Oct. 23, 1915.

An experiment, planned for a different purpose, illustrates that house-flies kept out of doors suffer from the disease. House-flies collected from time to time were placed in a large outdoor cage with abundant food, and kept there from July 7 to Sept. 23 when a considerable number of larvae and pupae were present. On this date the larvae were removed and placed in a galvanised iron box 2 feet square and $1\frac{1}{2}$ feet high, buried in the ground to a depth of 9 inches. The bottom consisted of perforated zinc and the interior was filled with earth up to the level of the surrounding ground. The top of the box sloped gradually to the centre where a circular opening 9 inches in diameter was situated. Above this opening a large cage of mosquito net, giving ample room for flies to move about in it, was suspended from the roof of a very large surrounding net cage ($6 \times 9 \times 6$ feet). The box, the small net cage above it and the outer net cage were proof against flies of moderate size. No adult flies were placed in the inner cage, and only the one batch of larvae and pupae just mentioned. This cage was known as cage I. The adult flies, the parents of the larvae, were collected on Sept. 26 and placed in a similar box provided with a small cage, cage II, and other house-flies were added frequently as they were caught. In the galvanised iron boxes food materials for the larvae were introduced at frequent intervals, and in the net cages syrup and water were provided for the flies.

The net cages above the boxes were about 3 feet apart and both were enclosed in the large net cage already mentioned, in which no flies had been confined since the previous autumn.

In cage I flies began to emerge on Sept. 24. About 60 flies were present on Oct. 7, and the total had reached 133 on Oct. 16. After this time the numbers gradually diminished though 100 were present on Nov. 7 and the last specimen died on Nov. 17.

Empusa first manifested itself in this cage on Oct. 11, two infected flies being found. The outbreak which followed may be divided into two parts, a period between Oct. 11 and Oct. 23 during which time 42 flies, or about 27 %, died of the disease, and a second period, commencing 16 days later, on Nov. 8, and lasting till Nov. 16, during which 43 flies, or about 43 %, present during this period died of the disease.

Many deaths occurred between Nov. 7 and 16 when the minimum temperature recorded by a thermometer on the grass ranged between 34° and 18° F.

The numbers of the flies present were counted at various times, the largest number present on one day being 133. Two hundred flies probably developed in this cage and 85, or about 40 %, died of the disease (Chart 8).

The flies in this cage had never come into contact with adult flies of any species large enough to be stopped by the mesh $\frac{1}{8}$ inch in diameter of the net of the outer cage, though some of the minute diptera may have gained access to their cage. Consequently it is quite clear that

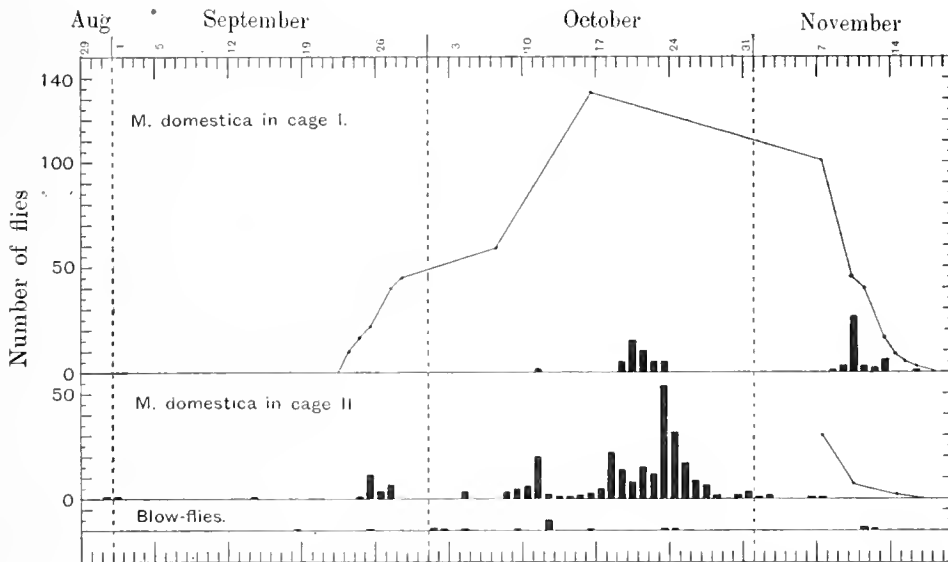


Chart 8. Showing the deaths (columns) from empusa disease amongst house-flies confined in cages I and II out-of-doors, and amongst blow-flies in a larger cage. The approximate numbers of house-flies present at different times in cage I are indicated by a thin line.

contact with infected adults of *M. domestica* is not essential for the transmission of the disease. We must assume, therefore, either that the infection took place in the larval stage before the larvae were placed in this cage (three cases had occurred amongst the parents), or that infection was carried by very small insects or mites which found their way into the cage, or lastly that the spores were carried by the wind.

Amongst the adult flies, first confined in a large cage and then put into cage II, the disease commenced on Aug. 31, but during the next 23 days only 3 cases occurred. After Sept. 24, however, cases occurred

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almost without interruption till Nov. 7, when there were still 30 flies alive, none of which subsequently developed the disease. The death rate reached its maximum between Oct. 18 and 25, the period during which the first outbreak was noticed in cage I. It may be worth noting that the disease had come to an end in cage II before the second outbreak occurred in cage I.

Altogether 1049 flies were placed in cage II and 281 or 26.7 % died with well-marked signs of the disease. It is quite possible that besides these some others died of the disease without showing recognisable signs.

Concurrently with these observations a careful watch was kept for the disease amongst the flies which entered various rooms in the house, and more especially amongst those which were allowed to live unmolested in the kitchen. Owing to their frequent migrations it was impossible to ascertain the percentage of flies in the kitchen which succumbed to the disease, but the mortality from the disease, as ascertained by noting cases of the disease indoors, seemed much smaller than amongst the flies kept out of doors. Possibly a number of those which migrated out ultimately died of the infection. Two cases occurred on Aug. 30, the date on which the disease started in the large fly cage. After this a long period elapsed before the next case occurred on Oct. 4. Three weeks later on Oct. 25 the first of a series of six cases, occurring between that date and Nov. 6, was noticed. Though flies were present in decreasing numbers up to Dec. 12 no other specimens with the disease were seen.

No previous attempt seems to have been made to ascertain with any degree of accuracy the mortality due to this disease.

Ample opportunities were afforded for observing the progress of the disease under natural conditions, and in some cases flies in the earliest stages were confined in glass boxes and watched. The first recognisable sign of the disease is an appearance of stiffness. The fly's legs are disposed in abnormal attitudes, and the insect is sluggish and remains in one place, though it is capable of moving in an awkward way when touched. Next white rings of growth begin to appear between the segments of the abdomen, but before the disease has made much further external progress the fly dies.

Under suitable atmospheric conditions the fungus grows with great rapidity after the death of the fly, and spores are discharged around the insect's body. A fly which only appears stiff and sluggish when attention is first attracted to it may show in 4 or 5 hours distention of the abdomen

with marked rings of white growth between the segments (Plate XXVIII, figs. 1-8), and within 15 hours a halo of spores may surround the specimen. If the fly is protected from wind currents the directions in which the spores are discharged are clearly indicated by the contour of the halo, as is shown in photographs of such specimens on Plate XXVIII, figs. 9, 10, 11. The spores seem to be discharged mostly from the abdomen, forming a well-marked eirele, incomplete only in front of the head, of a diameter of $1\frac{1}{8}$ inch round the fly. The spores may reach objects $\frac{1}{2}$ inch above the insect.

The growth of the fungus seems to be most rapid and complete in warm damp weather, but the optimum conditions of humidity and temperature have not been ascertained. On the other hand its progress may be fairly rapid even in cold weather, for on a fly confined in cage I, which first showed signs of infection on Nov. 16, marked white bands had developed by Nov. 18. During this time the maximum temperature recorded in the shade was 43° F., and the minimum on the grass varied between 20° and 22° F.

MITES.

In the course of these investigations two species of mites, one much larger than the other, came prominently to notice. Mr C. Warburton very kindly examined some of the specimens and reported that the smaller specimens were adults, belonging to the genus *Holotaspis*, and the larger, nymphs of the genus *Gamasus*, differing slightly from *G. coleopratorum*.

The *Holotaspis*, which seems to be parasitic, was found on several of the common species of flies, being especially frequent on the house-fly, *M. domestica*, *O. leucostoma* and *H. dentipes*. Often only a single parasite is found on a fly, attached in almost any situation. The anterior part of the ventral surface of the abdomen is a common situation, but the mite may be found on the thorax, head or leg. Specimens were even found attached between the eyes and on the distal end of the proboscis. Not infrequently, however, several are found on one fly, and then the individual mites may occur in different situations, or in a cluster. For example a specimen of *O. leucostoma* had one mite on the dorsum of the thorax, another at the base of the first pair of legs and a third at the base of the third pair, while one specimen of *M. domestica* had a cluster of four mites attached to the ventral surface of the abdomen, and another had a cluster of five on the upper surface of the thorax. In such cases the mites are often so close together that they appear

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to be standing on their heads. Some flies were kept in captivity in order to ascertain how long these mites remain attached to them. The longest period observed was 192 hours. It is very remarkable that the flies seldom seem to make any attempt to remove the mites wherever they are situated.

It may be of interest to note that numerous mites of this species were found on specimens of *M. stabulans* caught as early as April 26, 1916.

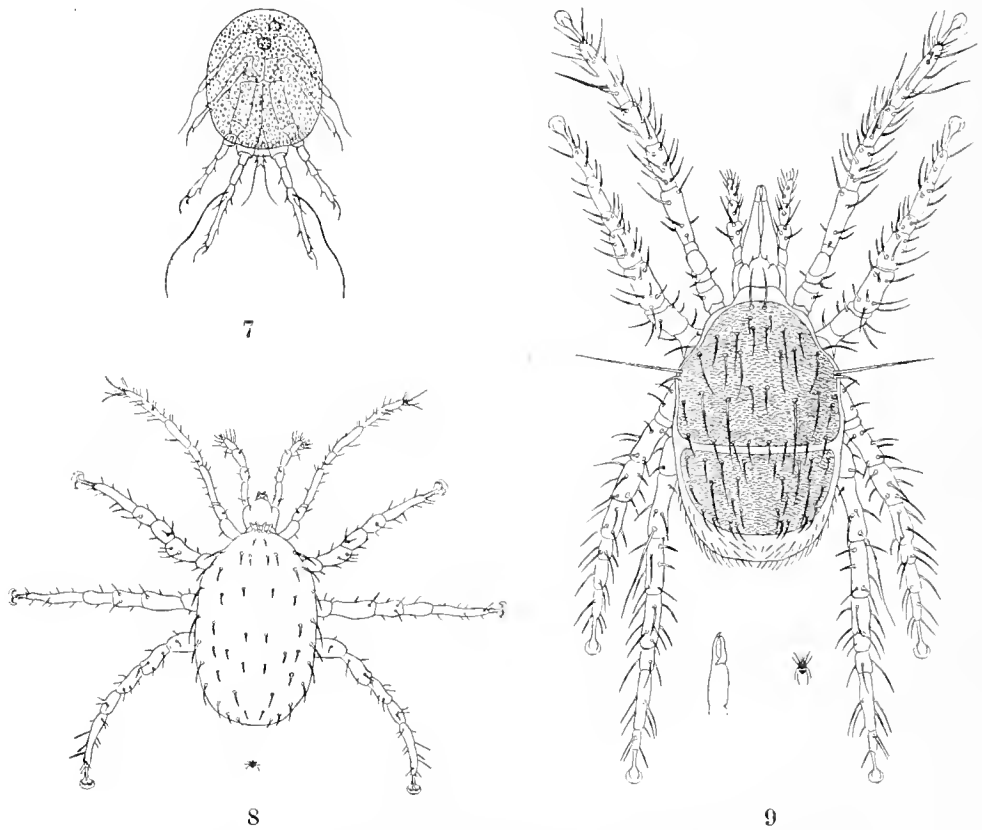


Fig. 7. Hypopial nymph of *Tyroglyphus siro* ($\times 50$) from *M. domestica*.

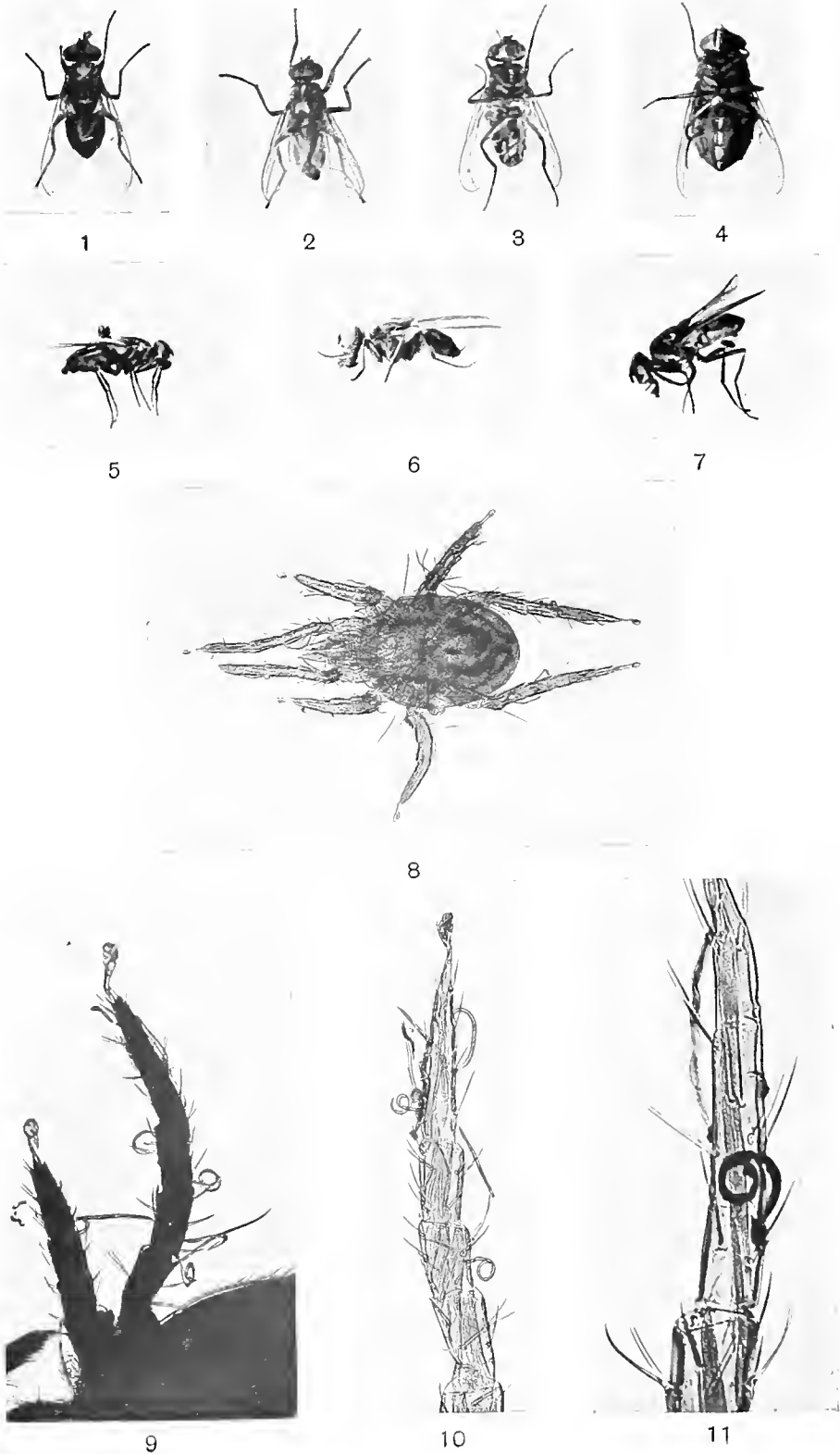
Fig. 8. *Holotaspis* sp. ($\times 30$ and nat. size) from *M. domestica*.

Fig. 9. Nymph of a *Gamasus* allied to *G. coleopratorum* ($\times 20$ and nat. size) from *C. erythrocephala*.

Several photographs of flies with mites attached in different situations are reproduced in Plate XXIX, figs. 1-7.

The *Gamasus* was present in great numbers, especially from August to October, on the remains of decaying animal matter on which larvae were feeding. Moreover they remained plentiful on such material throughout the following winter. They are occasionally seen on healthy flies, but do not seem to attach themselves permanently like the *Holotaspis* does,





and are probably not true parasites of the fly. On the other hand on several occasions a number were seen on weakly flies, which appeared to be dying and scarcely able to move. They were frequently seen, often to the number of eight or ten, under the bodies of dead flies, and seemed to be devouring them. In examining some of these mites caught on Nov. 19 on decaying animal matter, an interesting observation was made. Several had larval nematodes adhering to their legs, as many as eight worms being sometimes attached to a single leg. Occasionally the worms were attached to other parts of the mite. The mode of attachment was not clearly ascertained though a triangular mass of material staining with haematoxylin was always found on the surface of the mite at the point of attachment. The mass is probably secreted either by the mite or by the worm. This discovery was made late in the season, and no opportunity occurred of ascertaining whether blow-flies visiting the materials on which the infested mites were living became infected with the worms. Other examples of the same species of mite, collected from similar situations in the neighbourhood, were not thus infested, and the condition seemed to be very local. Dr C. L. Boulenger, who very kindly examined the worms, states that they are not the larvae of *Habronema muscae*, and that without rearing the adults it is impossible to determine the species.

On some of the flies examined hypopial nymphs (Fig. 7) belonging to the genus *Tyroglyphus* were found, and the adults of *Tyroglyphus siro*

Plate XXIX. Figs. 1-3, 5-7. Photographs of living specimens of *M. domestica* ($\times 2$) with mites of the genus *Holotaspis* attached to them. In fig. 1 a single mite is attached between the eyes, in fig. 2 two mites, seen as oval grey bodies, on the dorsum of the thorax, in fig. 3 three mites on the ventral surface of the abdomen, in fig. 5 two mites on the dorsum of the abdomen, in fig. 6 one mite on the anterior aspect of the proboscis, and in fig. 7 one mite on the ventral surface of the abdomen.

Fig. 4. Photograph of a living specimen of *C. vomitoria* ($\times 2$) with a nymph of *Gamasus* sp. attached between the bases of the hind legs.

Fig. 8. Photograph of the dorsal surface of a nymph of *Gamasus* sp. ($\times 15$) showing five nematodes attached to the leg projecting upwards and some on other legs.

Fig. 9. Photograph of a leg ($\times 30$) of a nymph of *Gamasus* sp. with six nematodes attached to it. Three are partly coiled, and the others extended.

Fig. 10. Photograph of a stained and mounted specimen of a leg of *Gamasus* sp. ($\times 45$) with six nematodes attached to it.

Fig. 11. Photograph of a stained and mounted specimen of a leg of *Gamasus* sp. ($\times 60$) showing a coiled nematode with a dark haematoxylin staining mass at the point of attachment, one extended nematode with a similar mass, and a dark mass on the edge of the specimen a short distance above the coiled nematode. A nematode became detached from this point during manipulation.

occurred in empty pupa cases. According to Michael (1901) the *Gamasidae* feed on the *Tyroglyphidae*, and it seems possible that some mites attach themselves to flies in order to feed on the hypopial nymphs, which so often adhere to the latter.

PSEUDO-SCORPIONS.

Occasionally small lobster- or scorpion-like creatures, about 2.5 mm. in length, are found clinging to the legs of flies. Though the records of their occurrence on flies go back for more than 150 years, it is, except in certain seasons, an uncommon event to find one attached to a fly. Judging from the published records, the house-fly is the species on which they are most frequently noticed. During the latter part of the summer of 1915 the writer was fortunate enough to find these creatures attached to different species of flies, and to make some observations on them. It may therefore be a fitting opportunity to give a short account of their structure and habits, and of the views which have been put forward to account for the very curious habit possessed by certain species of attaching themselves to flies.

These creatures are arachnids, belonging to the order *Chernetidea* (pseudo-scorpions). The body consists of a cephalothorax without segmentation in some groups, but with one or two dorsal striae in others, and an abdomen composed of twelve segments. The segmentation of the abdomen is emphasised by the presence of chitinous plates dorsally and ventrally, but the last two dorsal plates are fused, so that ordinarily only eleven segments can be counted dorsally and nine ventrally. The eyes, when present, are either two or four in number, and are placed near the lateral borders of the carapace towards its anterior end. They are whitish, and only very slightly convex, and are never situated on prominences (Warburton, 1909). Some species are without eyes. They possess pedipalpi, chelicerae and four pairs of legs. The chelicerae, which are two-jointed and small, bear certain interesting but minute structures, the galea, serrula and flagellum, used by some authorities on the group for the purposes of classification.

The very large, six-jointed pedipalpi, terminating in claws, give these animals their superficial resemblance to scorpions or lobsters. These structures have gained for them the popular titles of pseudo-scorpions or chelifers. About twenty species occur in Britain, some of which are stated to be common and widely distributed, but are seldom seen unless specially looked for in their haunts under stones, beneath the bark of trees or among moss, debris, decaying substances

and manure. One species, the "book scorpion" (*Chiridium muscorum*), usually lives in houses, but has been found in other situations.

Pickard-Cambridge (1892) conveniently divides the British species into three groups:

I. With four eyes, including the genera *Chthonius* (four species) and *Obisium* (three species).

II. With two eyes, including the genera *Roncus* (two species) and *Chelifer* (five species).

III. Without eyes, including the genera *Chernes* (five species) and *Chiridium* (one species).

This classification, though convenient, is not universally accepted (Kew, 1911). As might be expected from their small size and retiring habits little is known of their mode of life. Most species seem to be carnivorous, feeding on small insects. Many of them can run rapidly forwards, backwards or side ways, and some seem to be capable of jumping.

To the entomologist pseudo-scorpions are interesting chiefly on account of the extraordinary habit of seizing hold of flies' legs possessed by certain species. It is remarkable that this curious habit is almost confined to the blind species. Poda (1761) was apparently the first observer to refer to a pseudo-scorpion attached to a fly's leg, and a few years later Adams (1787) recorded the finding by Mr Marsham of one of these creatures "firmly fixed by its claws to the thigh of a large fly, which he caught on a flower in Essex the first week in August, and from which he could not disengage it without great difficulty and tearing of the fly's leg."

Since that time many notes, recording the occurrence of single pseudo-scorpions on the legs of house-flies in various parts of Europe, Algeria and America, have been published. Apart from such isolated statements, which throw little additional light on the subject, many interesting observations relating to the finding of several pseudo-scorpions on individual flies, and to their occurrence on various species of flies and other insects have been recorded. Donovan (1797) and Campbell (1887) each noticed a single pseudo-scorpion attached to a blow-fly (*Calliphora*), while Kirby and Spence (1826) state that these creatures are "occasionally parasitic upon flies, especially the common blue-bottle fly" (*M. vomitoria*).

An anonymous editorial note (*Entomological Mag.*) states that pseudo-scorpions were abundant under planks and bricks placed on decaying

vegetation in 1835, and that a small fly, *Lonchaea vaginalis*, common there in June was particularly infested by it. Loew (1845) "mentions having found in August 1841 another small fly, *Ulidia demandata*, running about in numbers on dry stems in a waste place on the parade-ground at Ofen, and so pursued by '*Chelififer corallorus*' that it was difficult to find specimens free from the attachment of this Arachnid."

Very rarely pseudo-scorpions have also been found attached to the legs of other species of flies, hover-flies and a species of *Anthomyia* (Gerstaecker, 1859), a species belonging to the *Dexiidae* (Banks, 1895), and daddy-long-legs (Hagen, 1879, and Wagner, 1892). Menge (1855) describes eight fossil species in Prussian amber, and reports the finding of one still attached to the leg of an ichneumon.

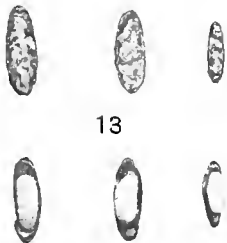
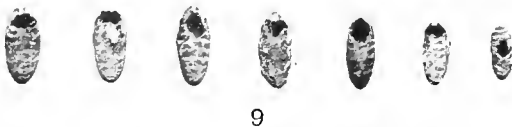
Certain kinds of pseudo-scorpions in several widely separated parts of the world have been found in the nests of bees, and they have been found associated with beetles, *Alaus oculatus*, and other species, especially in America. They do not, as far as is known at present, attach themselves to the legs of beetles, but occur on the dorsal surface under the wings. It has been suggested that they seek this situation in order to feed on the mites with which the beetles are often infested.

On two occasions pseudo-scorpions have been found attached to the legs of the long-legged false-spiders or harvestmen (Spicer, 1867, Leydig, 1867).

Instances in which two or more pseudo-scorpions have been found attached to a single fly are seldom observed. Both Hagen (1867) and Knab (1897) observed an instance of two chelifers attached to one leg of a house-fly, while Stainton (1864) saw a house-fly with three attached to one leg, and the same condition has been recorded in the case of *Lonchaea vaginalis* by the writer of the editorial note in the *Entomological Magazine* (1835). Löw (1866) noticed two attached symmetrically to opposite legs of *Ulidia erythrophthalma*. Knab (1897) and Stainton (1864) have noticed three on one house-fly, and Stevens (1866) observed one house-fly with six chelifers clinging to it and another with eight. Hagen (1867) even states that ten have been found on a single fly. Loew (1845) mentions that some of the *U. demandata* observed by him were beset with three or more pseudo-scorpions, Schiner (1872) reported the capture of a specimen of this species with five chelifers attached to it, and the writer of the editorial note in the *Entomological Magazine* (1835) refers to the attachment of as many as four to the legs of *Lonchaea vaginalis*.

In some years pseudo-scorpions are more commonly found attached





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to flies than in others, Stainton for example noticing unusual numbers in 1865, and Hill stating that they were very commonly found on flies near Eton in 1905. According to the writer's observations flies bearing pseudo-scorpions were common in 1915.

"As regards the kinds of pseudo-scorpions in which the habits above noted obtain, it must be remembered that with animals of the present kind names, in the hands of writers other than specialists, have not the value they usually possess in more familiar departments of Zoology. *Chelifer cancroides*, for instance, derived from the Linnean *Acarus* or *Phalangium cancroides*, was long a stock name for pseudo-scorpions of any kind; and its use, more especially by earlier writers, rarely implies any attempt at specific discrimination.... The German arachnologist L. Koch states his experience that the species found attached to flies is always *Chernes Reussii* C. Koch = *Chernes nodosus*.... Stecker (1875), referring to this remark, states that *Chernes cimicoides*, not *Chernes nodosus*, occurred to him under these conditions. All the European pseudo-scorpions found on flies' legs by Simon and by his correspondent Mr Ray, of Troyes, proved to be *Chernes nodosus*; and Mr Cambridge, in England, who does not mention the finding of any other species thus situated, states that all, or nearly all, of the individuals

Plate XXX. Fig. 1. Photograph of a living specimen of *S. calcitrans* (nat. size) with *C. nodosus* clinging to the tarsus of the left back leg. Fig. 2. Photograph of a living specimen of *O. leucostoma* (nat. size) with *C. nodosus* clinging to the tibia of the left back leg. Fig. 3. Photograph of a living specimen of *M. domestica* (nat. size) with *C. nodosus* clinging to the tarsus of the right back leg. It will be seen that in each of these cases the pseudo-scorpion is attached by one claw only. Figs. 4 and 5. Photographs of a living specimen of *M. domestica* (nat. size) with *C. nodosus* clinging near the base of the right middle leg. In fig. 4 the fly is seen in the act of cleaning its left wing between two legs, and in fig. 5 is rubbing its two front legs together. Figs. 6 and 7. Photographs of the dorsal and ventral surfaces of *C. nodosus* ($\times 15$). Fig. 8. Five puparia (nat. size) of *C. erythrocephala* showing the circular and vertical splits produced when the flies emerged. Fig. 9. Seven puparia (nat. size) from which braconids, *A. manducator*, have emerged by gnawing irregular oval openings. Fig. 10. Seven puparia (nat. size) from which chalcids, *M. acasta*, have emerged by gnawing minute round holes. In the left-hand specimen the hole is near the centre, and in the next five near the anterior end. The right-hand specimen shows two holes. Figs. 11, 12. Photographs of living specimens (nat. size) of *A. manducator*, which emerged in the autumn. Fig. 13. Photographs of three pupae (nat. size) opened longitudinally to show numerous living larvae of *M. acasta* within them. Fig. 14. Photograph of three pupae (nat. size) opened longitudinally to show a single living larva of *A. manducator* in each. Figs. 15 and 16. Enlarged photographs ($\times 2.3$) of the left-hand and middle specimens shown in fig. 13. Most of the numerous small shining larvae are clearly seen, but some specimens which moved during the exposure are slightly blurred.

of *Chernes nodosus* communicated to him from different parts of the country were obtained from the legs of flies" (Kew, 1901). In a recent paper Kew (1911) states that *C. nodosus* "often comes to notice on flies' legs in Autumn," and mentions that *C. Godfreyi* has been found once attached to a fly by H. Hill (1907) but mistaken for the former species. During the summer and autumn of 1915 the writer observed specimens of *C. nodosus* attached to flies on several occasions. On Sept. 7 a specimen of *M. domestica* was caught with three of these pseudo-scorpions attached to its legs; while on Sept. 12 out of sixty-four house-flies which entered a room facing west two had single pseudo-scorpions attached to their legs. On Oct. 3 twenty-five house-flies entered this room, and one had a pseudo-scorpion clinging to the base of the tarsus of one leg, and on Oct. 20 another house-fly entered this room with a chelifer attached to its leg. A specimen of *Ophyra leucostoma* was caught outside on Sept. 5 with one specimen of *C. nodosus* and three mites attached to it; and on Aug. 3 a female *L. vaginalis* with two pseudo-scorpions symmetrically attached to opposite legs. A specimen of *C. nodosus* was also received on Oct. 15 which had been found on a female *M. corvina*. The most interesting capture, however, made on Oct. 16, was a *Stomoxys* with two specimens of *C. scorpoides* Herm. attached symmetrically to the femora of the middle legs. This appears to be the first time that this chelifer has been found on a fly in Britain.

Kew (1911) gives the following descriptions of the chelifers which have been found attached to flies in Britain.

Chelifer nodosus Schr.

"*Chelifer nodosus* Schr., 1803. *C. inaequalis* Curtis, 1849. *Chernes Reussii* (C. L. Koch), L. Koch, 1873. *Chelifer nodosus* (Schr.), Simon, 1879.

Palps and cephalothorax reddish-brown, abdominal tergites olive-horny; glossy, with nearly simple bristles. Cephalothorax weakly granulate at sides, dorsum non-granulate, second groove scarcely perceptible or absent; abdominal tergites non-granulate reticulate, scar-spots indistinct, main sclerites near inner margin with 1-3 bristles in front of row, tergite sternite XI with two pairs of tactile hairs, tergite with inner pair considerably shorter than outer; galea (♀) well developed, branching from short base, branches simple rather long; palps trochanter with upper protuberance distinctly dorsal, lower protuberance alone projecting posteriorly, its proximo-posterior corner moderately prominent but distinctly rounded, tibia strongly convex in front, hand (♀) moderately broad obliquely high, anterior margin of fingers with an isolated accessory tooth; the palp is granulate, at least in front, with small part of femur and great part of tibia and hand smooth; lower face of maxillae smooth; coxae IV (♀) short and broad, inner margin longer than posterior; legs IV

tibia with tactile hair near extremity (shorter than that of tarsus), tactile hair of tarsus about one-third removed from base. ♂ with galea poorly developed, hand somewhat narrower with less oblique height, coxae iv differing little from ♀. L. 1-7.

Among vegetable refuse: in cucumber frames, manure-heaps, etc.; widely distributed and common in Britain; probably also in Ireland, but not yet recorded; seizes flies and often comes to notice on their legs in autumn; a mysterious animal of which males are seldom seen.

C. Godfreyi sp. nov.

Palps and cephalothorax reddish-brown, abdominal tergites olive-horny: glossy with nearly simple bristles. Cephalothorax weakly granulate at sides and over part of dorsum of thorax, dorsum of head non-granulate, second groove scarcely perceptible or absent: abdominal tergites non-granulate reticulate, scar-spots indistinct, main selerites near inner margin with one bristle in front of row, tergite-sternite xi each with two pairs of tactile hairs, tergite with inner pair not greatly shorter than outer; galea (♀) well developed, branching from short base, branches simple rather long; palps trochanter as in preceding species, tibia less strongly convex in front, hand with somewhat less oblique height, anterior margin of fingers with an isolated accessory tooth; the palp is granulate, at least in front, with small part of femur and great part of tibia and hand smooth; coxae iv short and broad, inner margin longer than posterior; legs iv tibia with tactile hair near extremity (as long or almost as long as that of the tarsus), tactile hair of tarsus further from base than in preceding species; taking only dorsal margin about in middle. ♂ with galea poorly developed, hand somewhat narrower with less oblique height (?), coxae iv differing little from ♀. L. 1-6.

Found in manure-heaps and moss."

The two species just described are closely allied; but the next was distinguished from *C. nodosus* by the naked eye when clinging to the fly, by its woolly appearance.

C. scorpoides Herm.

"*Chelifer scorpoides* Herm., 1804. *Chernes phaleratus* (Simon), Camb., 1892; by mistake. *Chernes minutes* Ell., 1896. *Chelifer scorpoides* (Herm.-Töm), Ell., 1907.

Palps and cephalothorax reddish-brown, abdominal tergites horny-brown; dull or nearly so, with clavate and toothed bristles. Cephalothorax granulate, both grooves distinct; abdominal tergites granulate with moderately long distinctly clavate bristles, scar-spots indistinct, interstitial membrane of dorsum wrinkled sternites with bristles simple or nearly so, tergite xi with one pair sternite xi with two pairs of tactile hairs; galea (♀) well developed, staghorn-like, branching from broad short base, branches redividing; palps rather stout, tibia strongly convex in front, anterior margin of fingers with an isolated accessory tooth; the palp is granulate all round, including hand, fingers granulate, bristles of front femur moderately long, a little clavate; lower face of maxillae weakly granulate; coxae iv (♀) short and broad, inner margin as long as or longer than posterior; legs iv tibia

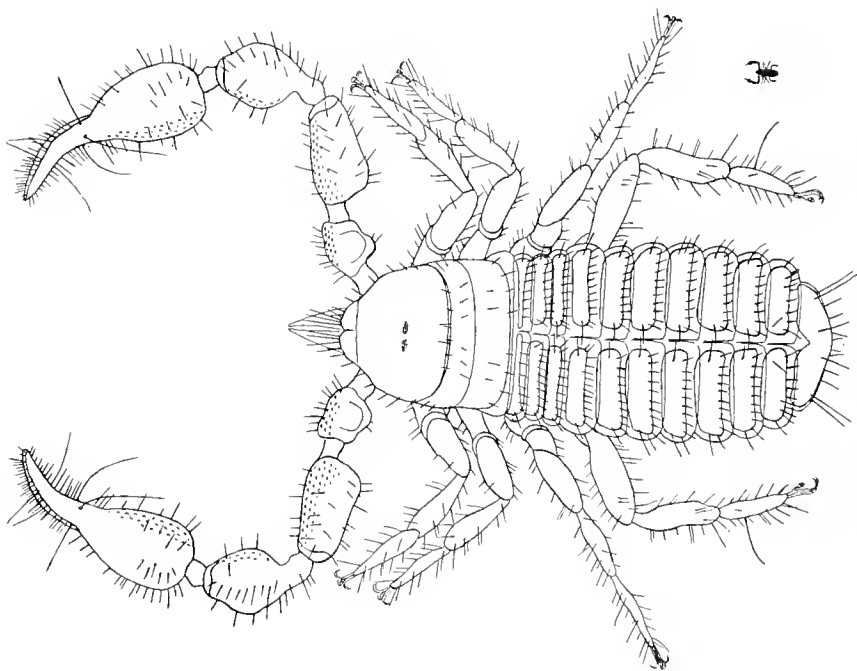


Fig. 10. *C. nodosus* ($\times 25$ and nat. size) from
M. domestica.

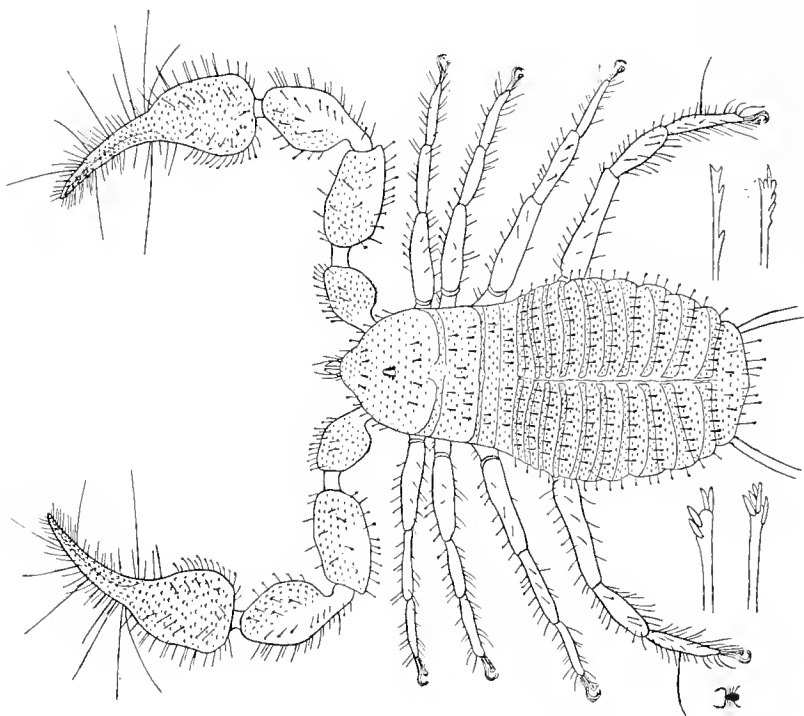


Fig. 11. *C. scorpioides* ($\times 25$ and nat. size) from *S. calcitrans*.
Four bristles greatly enlarged.

without taetile hair, taetile hair of tarsus near middle. ♂ with galea poorly developed, hand a little narrow, coxae iv differing little from ♀. L. 1.7.

Among vegetable refuse, in rubbish heaps, etc.; sometimes abundant; probably widely distributed: Essex, Kent, Surrey, Sussex; also about decaying trees: New Forest; in nests of *Formica rufa*; in nests of *Bombus muscorum*."

Several views have been put forward to account for the habit of seizing flies.

(a) Some have regarded the pseudo-scorpions as parasites which obtain nourishment from the bodies of the living flies. In the majority of carefully observed cases no injury to the leg of the fly was noticed and there is little evidence that the creature makes its way up the leg to the body in order to reach the less chitinous parts of the fly, though occasionally it is found attached to the body and not to the leg. Donovan (1797) noticed one "fastened on to the body of *Musca vomitoria*, the common flesh-fly, from which it could not be extracted without killing and tearing the fly to pieces," and Kirby and Spence (1826) state that "they adhere to it (the common blue-bottle fly) very pertinaciously under the wings."

(b) According to another view the pseudo-scorpion is predaceous, remaining attached to the fly until the insect dies and then sucking its juices. Undoubtedly the pseudo-scorpions cling to flies with great tenacity and the latter, although they constantly make efforts, seldom seem to succeed in getting rid of them. Even when the fly is captured and handled the pseudo-scorpion seldom relaxes its hold. Moore (1835), however, once saw a pseudo-scorpion voluntarily drop from a fly. Hess observed a chelifer hanging on to a fly's leg without altering its position for 56 hours, and Stainton (1864) stated that in his experience the chelifers did not quit the flies until the latter died. Lukis (1831) on one occasion saw a chelifer dragging about the dead body of a *Stomoxys*. Backhausen made some very interesting experiments which seem to support this view. He placed a fly with a pseudo-scorpion hanging to one leg under a glass. Next morning he found the fly dead and the pseudo-scorpion fat and bloated under some scraps of paper.

"He next placed ten pseudo-scorpions on a tray with earth and leaves, put them under the glass, left them for a few days without food, and then imprisoned a few small flies. As soon as the pseudo-scorpions perceived the presence of the insects they came out of hiding and began to snatch at them, attaching themselves to their legs, always with one pincer, but using the other in their endeavours to obtain an assured holding. Once fixed they continued to hold to the leg." The

observer was somewhat hindered by want of appliances, but he states that the flies died while the pseudo-scorpions remained on the legs and "that after the flies' death the creatures travelled along the legs to the body, and finally drew the insects under the leaves to suck out their juices."

Experiments of this kind should be repeated, under more natural conditions, the pseudo-scorpions and flies being supplied with their accustomed food.

(c) Another view is that the chelifers resort to flies in order to feed on the parasitic mites (Hickson, 1905; Pocock, 1905). Though chelifers may resort to beetles for this purpose, it seems clear that this is not the reason for their attaching themselves to flies, since many of the flies to which chelifers cling have no visible mites on them. Very small hypopial nymphs are said, however, to be frequent on flies, and would pass unnoticed unless carefully looked for.

(d) The dispersal hypothesis, which has the support of many observers, claims that the chelifers cling intentionally to flies in order to be transported from one feeding ground to another. Others, however, think that the seizure of the fly's leg is either accidental, the chelifer mistaking it for some small insect suitable for food, or through irritation at being disturbed.

"The attachment, whether intended or accidental, obviously serves for dispersal; but it is probable that it is not a means of dispersal only, the phenomena having, almost certainly, a further significance."

The writer carefully observed some of the infested flies he caught, and in view of the various hypotheses, which have been discussed, these observations may be of some interest. The chelifer always grasped the fly's leg by one claw and was never seen to make any attempt to seize it with both, or to climb up the limb towards the body. The house-fly with three chelifers attached to it caught on Sept. 7 was placed in a glass box. By the next day two of the arachnids had relaxed their hold, and were crawling about the box. They never made any attempt to seize the fly again although the fly frequently walked over them. The other remained clinging to the fly till the insect was killed on the 9th (48 hours). The house-fly caught on Oct. 3 with a chelifer attached to the base of its tarsus was kept in a glass box for 4 days. During the whole of this time (90 hours) the chelifer remained attached in the same position. On the evening of the 4th day, however, it dropped off, but soon reattached itself to the back of the fly near the junction of the thorax and abdomen. After a time the fly managed to remove it

and the next day the chelifer appeared to be dead. The house-fly caught on Oct. 20 with one chelifer attached to a leg was also kept in a glass box. On the following morning the chelifer dropped off, but towards the evening it attached itself again. During the second night it left the house-fly and attached itself to the leg of a *Stomoxys*, which had been placed in the same box. It remained in this position till the *Stomoxys* died about 36 hours later, and was still attached in the same position some hours after its death.

It was noticed that the chelifers occasionally came off when the flies to which they had been attached were confined in glass vessels. Sometimes this appeared to be a voluntary act on the part of the chelifer, but on other occasions the fly got rid of the chelifer by means of its legs. The fly most commonly succeeded in detaching the chelifer when it got into a confined space, and was able to use its legs with greater effect than under natural conditions. Usually the detached chelifer made no attempt again to seize the fly though the fly often passed over it. When undisturbed it often walked forwards swaying its pedipalpi from side to side, and sometimes opening and shutting the claws, but occasionally stopping and bringing one of its claws to its mouth. At the approach of the fly it either ran backwards rapidly, or remained quite still. When touched by the fly's legs it seemed to be greatly irritated. On two occasions, however, detached chelifers were seen to seize the legs of flies. The movement was very rapid, the chelifer appearing to spring towards the fly's leg as the insect was approaching.

All interested in this subject should consult Kew's (1901) interesting paper.

PARASITES OF FLY LARVAE AND PUPAE.

During the autumn of the year 1914 flies were allowed to deposit their eggs on the carcasses of small animals. Some of these carcasses were allowed to remain undisturbed on the ground through the winter in an outdoor cage, and others, laid on earth, were placed in two large galvanised iron receptacles into which flies could enter freely. One of these iron receptacles was kept in an open situation, where it was exposed to the extremes of heat and cold, and the other in a shady protected situation, where it never became very hot. These may be called the "Sun and Shade Tins" respectively (see p. 442). In the winter the minimum temperature recorded in the "sun tin" was usually about 1-2° F. below that in the "shade tin"; on the other hand

the maximum temperature, especially in the spring, was not infrequently many degrees higher in the "sun" than in the "shade tin." The daily variations in temperature were therefore much greater in the "sun" than in the "shade tin."

On April 11, 1915, the earth containing the pupae was collected from the bottom of each tin and placed in a small wooden box with a balloon trap fixed over an opening in the lid. The box was replaced in its tin. The object of this procedure was to catch any flies which might emerge from the pupae, but at the same time to leave the pupae in their respective tins in which slightly different conditions prevailed. On April 22 Anthomyid flies began to emerge in both boxes, and on April 23 blow-flies. The blow-flies emerged in great numbers from the "shade box" and continued to do so up to May 11; altogether 987 blow-flies, 58 *F. scalaris*, 10 *H. dentipes*, 12 *T. canescens* were obtained from this box. In the "sun box" on the other hand only 16 blow-flies and one small fly emerged between April 23 and May 2. After the flies had ceased to emerge numbers of large braconids made their appearance. Between May 15 and 29 twelve of these braconids emerged in the "sun box," while between May 17 and June 16 at least 209 emerged in the "shade box." As a few managed to escape through the mesh of the trap the complete total is unknown in each case.

After this a period of three months elapsed in which neither flies nor braconids emerged, but on Sept. 19 further braconids commenced to emerge in the "shade box" and continued to do so until Oct. 15, at least 1115 appearing during this period.

As this observation is of some interest, and may be of some importance, Chart 9 is inserted showing the dates on which the braconids emerged.

The individuals emerging in the spring were much larger than those which emerged in the autumn. Males and females emerged both in the spring and autumn. (See p. 531.)

No braconids emerged from the "sun box" after May, and no second batch of flies emerged from either box.

Mr G. T. Lyle very kindly identified these braconids as *Alysia manducator*, and stated that those which emerged in the spring and the autumn belonged to the same species.

On various occasions this species of braconid was seen laying eggs on large maggots feeding on carcasses of large and small animals, but no evidence was obtained that they are capable of ovipositing in pupae. There can be therefore little doubt from the conditions under which

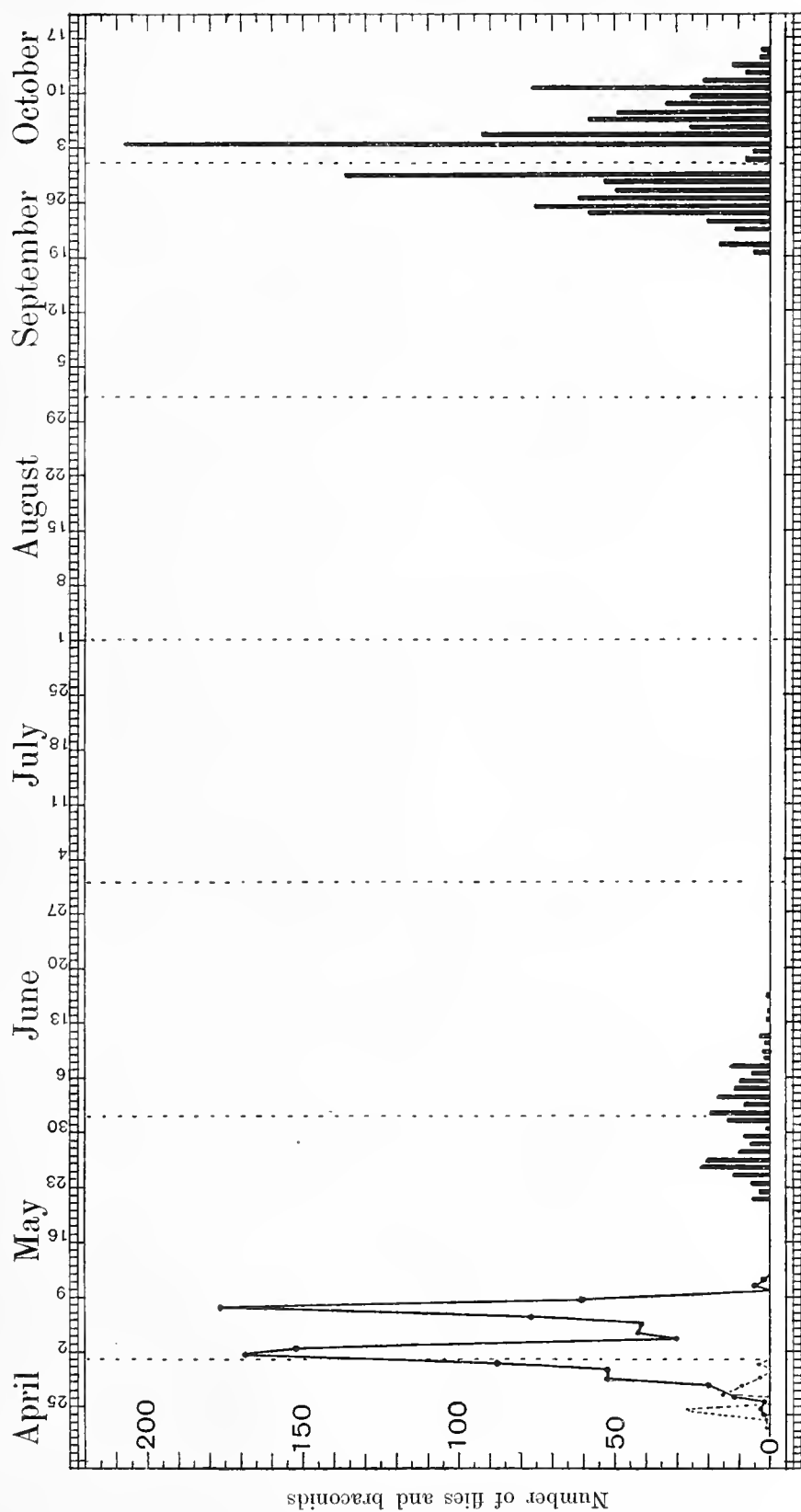


Chart 9. Showing the numbers of flies (*F. scalaris* dotted line, *C. erythrocephala* continuous line) emerging from 1914-15 winter pupae in the "Shade Tin," and the braconids, *A. manducator* (columns), appearing in the spring and the autumn of 1915.

the experiment was made that both sets of parasites emerged from eggs deposited in the autumn of 1914, for there was little chance of wild braconids gaining entrance to the box in which the pupae were kept, and those which emerged were collected and killed each day.

A point of some interest is that the first batch of braconids began to emerge just at the time when blow-flies reared from pupae, which had wintered in the earth, commenced to lay eggs, and the parasites therefore appeared when larvae were becoming numerous. The second batch

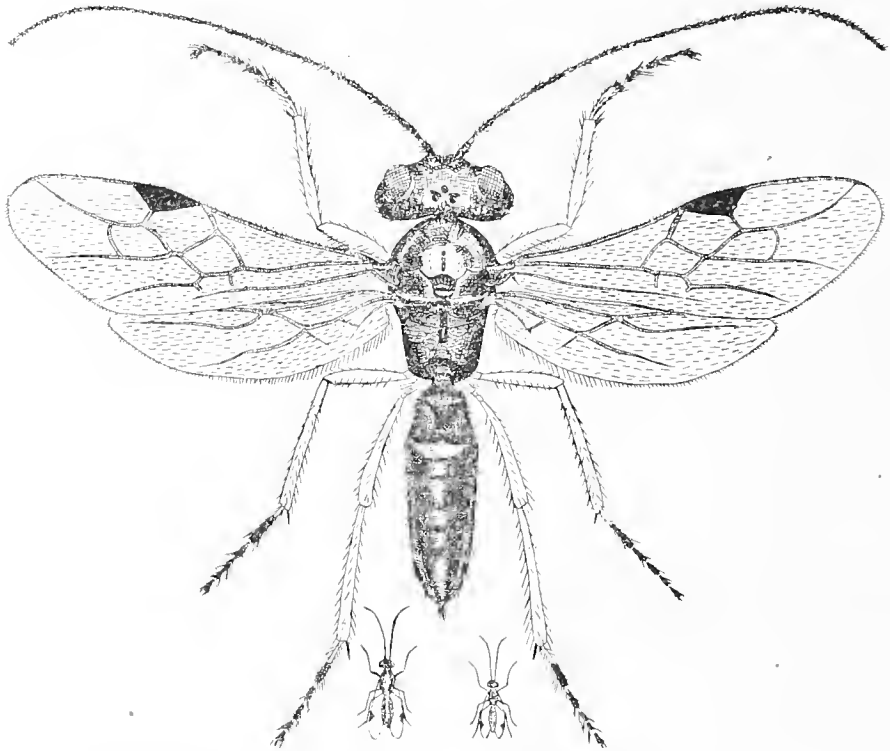


Fig. 12 *Alysia manducator* ($\times 6$) from pupa of *C. erythrocephala*. The lower left-hand figure represents a specimen (nat. size) which emerged in the spring, and the right-hand figure one (nat. size) which emerged in the autumn.

appeared about the time that the autumn larvae, which spend the winter as pupae, are found (see p. 461).

The same species of braconid were also obtained in May, 1915, from blow-fly pupae dug up from earth in which they had pupated under natural conditions in the autumn of 1914. The pupae were taken from the earth on April 24, before any flies had emerged, and kept in a room. The braconids commenced to appear from them on May 29.

When the great difference in the number of flies emerging from the two boxes became apparent, an experiment was tried to ascertain whether the difference was due to the effects of the somewhat greater cold during the winter in the exposed "sun tin," or to the effects of the high temperatures or great daily oscillations in temperature developed in that "tin" by exposure to the sun in the spring months.

For this purpose on April 29, 1915, a number of pupae were removed from the "shade box" and placed in a separate receptacle in the "sun tin," and some from the "sun box" were similarly placed in the "shade tin." It was found that flies and braconids continued to emerge from the pupae transferred from the "shade" to the "sun tin," but that none emerged from those transferred from the "sun" to the "shade tin." At first sight it seemed evident that it was the difference in the winter conditions which influenced the pupae. Further observation showed, however, that this was an erroneous conclusion and that the difference was due to further parasitism by chalcid parasites (p. 529).

On May 6 some of the unbroken pupae from the "sun box" were examined, and nearly all were found to contain single living braconid larvae in an advanced stage of development. On May 22 pupae from the "shade box" were examined; the larger ones were empty, blow-flies and braconids having emerged from them, but the medium sized and small pupae contained braconid larvae as in the "sun box."

In November, 1915, as there did not seem to be any prospect of further flies emerging from these boxes, the puparia in each were carefully examined.

On comparing the puparia remaining in the boxes with specimens from which either flies or braconids had emerged, it was not difficult to ascertain whether a fly or a braconid had emerged from a given puparium. In the act of emerging a fly pushes off the anterior end of the puparium in a characteristic fashion (see p. 449). On the other hand the braconid emerges by gnawing an irregular oval hole near the anterior end of the puparium (Plate XXX, fig. 9). A single specimen of *A. manducator* emerges from each puparium. In many examinations of puparia just before the emergence of the parasite it was found that the head of the braconid was always at the anterior end of the puparium.

Puparia from which flies and braconids have emerged can also be differentiated in another way. A puparium from which a fly has emerged is lined by a very thin, almost transparent, brittle membrane;

whereas one from which *A. manducator* has emerged is lined by a thick, yellowish, tough membrane, leaving a ragged edge when torn. Puparia containing shrivelled or moist decomposing fly remains are very brittle and unlike those which contain braconid larvae.

Large numbers of puparia ruptured in both these ways were found and counted, but besides these there were also found puparia which showed no signs of any opening, and many others, each perforated by a minute, round hole like a pin-prick. In the former either the shrivelled remains of fly pupae or living chalcid larvae were found, and in the latter some dead chalcids, and dry, dusty fragments on which numerous small mites, apparently *Tyroglyphus siro*, were feeding. The examinations of the puparia revealed much that was of interest and worthy of detailed record.

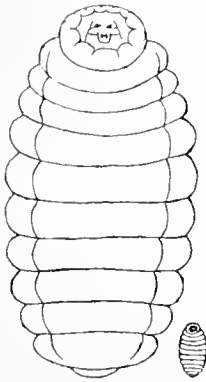
A. In the "shade box" the remains of 2778 puparia were found. From these 1067 flies (987 blow-flies, 58 *F. sealaris*, 10 *H. dentipes*, 12 *T. canescens*) had emerged, 9 puparia contained shrivelled, moist or decomposing fly remains. 1324 braconids had emerged and had been caught, 66 puparia contained dead braconids, and from 304 puparia braconids had emerged and escaped. Lastly five puparia contained living braconid larvae, and three were being eaten by unknown larvae. Therefore of all the pupae originally in this tin 61 % had been parasitised by braconids. The examination of the pupae in May revealed the interesting fact that the large braconids which had appeared previous to that time had emerged from the largest puparia, almost all of which were empty. The smaller specimens of the same species which emerged in the autumn came therefore from the medium sized and smaller pupae.

B. As previously stated a batch of pupae were transferred from this box to the "sun tin" on April 29 and kept there in a separate jar. This jar, on examination in November, was found to contain 293 puparia. From these 17 flies (14 blow-flies and 3 *H. dentipes*) had emerged, 28 puparia contained shrivelled or putrifying fly remains, 60 braconids had emerged, 4 puparia contained dead braconids, 23 puparia showed pin-holes and contained dead chalcids, and 161 puparia were whole and contained chalcid larvae. In this jar therefore 21.8 % of the pupae were parasitised by braconids and 62.6 % by chalcids. Since no chalcids were present in the original stock of pupae it is clear that the parasitism by the chalcids took place after the transferred pupae were placed in the "sun tin."

C. In the "sun box" the remains of 971 puparia were found.

From these 17 flies (16 blow-flies and 1 small fly) had emerged, 74 puparia contained shrivelled or putrifying fly remains, 180 braconids had emerged, 7 puparia contained dead braconids, 349 showed pin-holes and contained dead chalcids, and 344 were whole and contained living chalcid larvae. In this box therefore 19.2 % of the pupae were parasitised by braconids, and 71.3 % by chalcids.

D. From this "box" a batch of pupae were transferred on April 29 to the "shade tin" and kept in a separate jar. This jar contained 47 puparia. From these one blow-fly and a living braconid emerged, and of the 45 remaining puparia 5 contained shrivelled fly larvae, 1 contained a dead braconid and 39 contained living braconid larvae¹.



13



14

Fig. 13. Larva of *A. manducator* ($\times 6$ and nat. size) removed from a puparium of *C. erythrocephala*.

Fig. 14. Chalcid larva ($\times 20$ and nat. size), probably *M. acasta*, removed from a puparium of *C. erythrocephala*.

In this jar therefore 87 % of the pupae were parasitised by braconids. The reason for the retardation in the development of these parasites is not clear.

The last two observations confirm the view that the chalcid infection occurred after April 29, and further it seems justifiable to conclude from these four experiments that the chalcids only frequent warm or sunny places. The extent of autumnal infection with braconids, uncomplicated by subsequent chalcid infection, in the two tins is shown by the results of the examination of the puparia in the "shade box,"

¹ Of these 39 puparia 21 were examined and contained braconid larvae. The remaining 18 probably also contain them and have been kept in order to observe further developments, if any. One opened on June 2, 1916 contained a recently formed braconid pupa.

and in the jar transferred from the "sun" to the "shade tin." In the former it is 60 %, in the latter nearly 90 %. That the latter figure is a true index of the extent of braconid infection in the original stock of pupae is shown by the fact that 9 % of the pupae in the "sun tin" were not parasitised.

These facts reveal the extraordinary destruction wrought by these parasites, and indicate that larvae feeding in warm and sunny situations are more liable to attack than those living in shady places.

It may be argued that in these experiments natural conditions were not simulated sufficiently closely and that the braconids enjoyed unusually favourable opportunities. Other evidence, however, shows

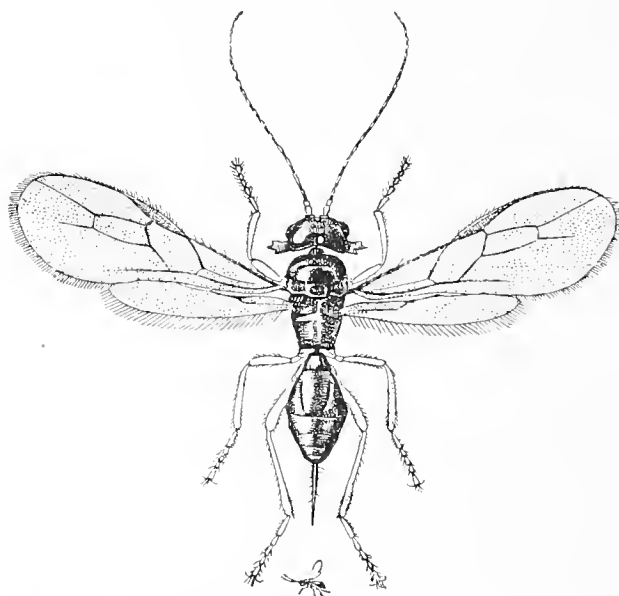


Fig. 15. *Aphaereta cephalotes* Hal. ♀ ($\times 11$ and nat. size) from pupa of *S. melanura*.

that under natural conditions a great destruction of the fly larvae results from braconid infection. In the autumn of 1914 very large numbers of blow-fly larvae were present in two experimental cages previously described (p. 443). Yet in the spring of 1915 only 308 and 206 blow-flies emerged in these cages. The number of pupae was not ascertained, but very numerous braconids are known to have emerged. Another experiment carried out in the winter of 1912-13 tends to confirm this view. Several samples of dog excrement containing *sarcophagid* larvae were placed in jars in the autumn of 1912. The mouths of the jars were covered with muslin, and they were kept outside until the spring of 1913. The pupae in the jars were then

collected and kept under close observation. From many of the pupae flies, identified by Mr P. H. Grimshaw as *S. melanura* Mg., emerged, but from others large numbers of small braconids, identified by Mr G. T. Lyle as *Aphaereta cephalotes* Hal., appeared. Three of the parasitised pupae, for example, contained 10, 13 and 14 braconids respectively.

Further experiments were carried out during the winter of 1915-16, and some interesting additional information has been obtained. On January 29 a batch of 114 out of the very numerous pupae, which have passed the winter of 1915-16 in the "sun tin," were placed in jars in the kitchen (room E), where the mean daily temperature is about 60° F. Between March 3-18 29 flies (18 *C. erythrocephala*, 9 *F. manicata*, and 2 *N. cylindrica*) emerged, and between March 18-25 33 large braconids, *A. manducator*, 21 ♂ and 12 ♀. Also between March 23-29 67 small braconids, *Aphaereta cephalotes*. By keeping pupae in separate tubes it was ascertained that in this species the proportion of males to females emerging from different puparia varies greatly. From one puparium 1 ♂ and 8 ♀ emerged, from a second 2 ♂ and 8 ♀, from a third 2 ♂ and 8 ♀, from a fourth 1 ♂ and 3 ♀, from a fifth 3 ♂ and 4 ♀ and from a sixth 6 ♂. It may be noted that puparia from which *A. cephalotes* have emerged are not lined by the thick tough membrane produced by *A. manducator*. Thirty-eight pupae remain from which braconids, corresponding to the autumn batch of 1915, will doubtless emerge. Some of these opened on May 31 contained larvae of *A. manducator*. The factors which retard the development of these larvae have not been ascertained.

Other pupae from the same source were kept at different temperatures (see Table I, p. 456). *A. manducator* (12 ♂ and 1 ♀) emerged from pupae in room A between April 25 and May 16, and in rooms B (36 ♂ and 6 ♀), C (13 ♂ and 3 ♀), and D (13 ♂ and 7 ♀) between April 7 and May 5. In the "sun tin" 678 ♂ and 160 ♀ emerged between April 9 and May 30, and in the "shade tin" 132 ♂ and 59 ♀ between May 17 and June 1. From these observations it appears that the emergence of the spring batch of *A. manducator* is greatly influenced by the temperature, and that under all conditions the males appear before the females. *A. cephalotes* emerged in rooms A (6 ♂ and 12 ♀) and B (11 ♂ and 29 ♀) and in the "sun tin" (185 ♂ and 454 ♀) after *A. manducator* had almost ceased to appear. In the "shade tin" this species commenced to emerge on June 1. *A. cephalotes* had parasitised relatively few of the pupae.

Careful study of this subject might reveal new and important facts, which might be utilised in the artificial control of flies of various species.

The chalcids, discovered in the 1914-15 winter puparia, which Mr J. Waterston¹ very kindly examined, belonged to two species, one of them occurring very rarely. The species, most commonly found, *Melittobia acasta* Wlk., proved to be of great interest (Figs. 16, 17). It only occurred in puparia from the "sun tin," both those which had been there throughout the winter and those which were taken from the "shade box" and placed there on April 29. From the facts which have been given there can be little doubt that this parasite attacked the puparia after the beginning of May. A large number of puparia from this source, which either appeared to be intact or which had

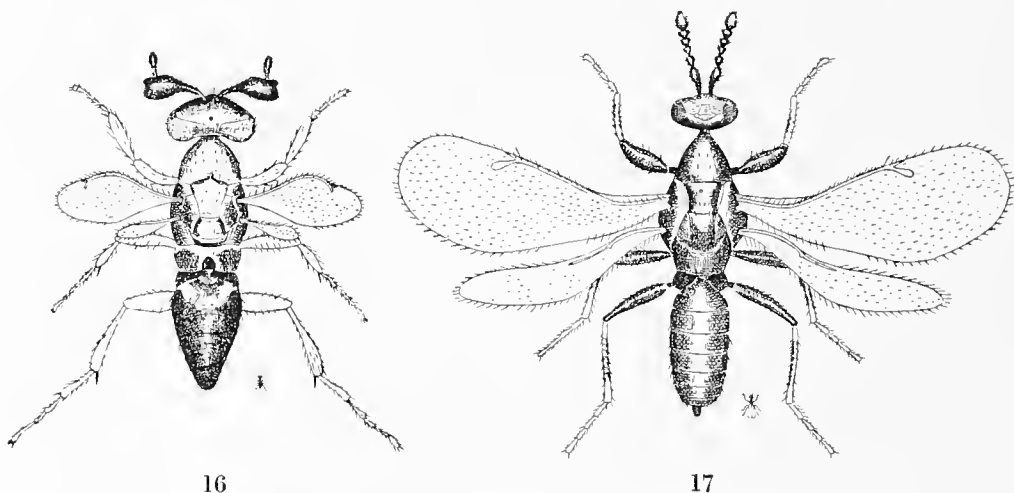


Fig. 16. *Melittobia acasta* Wlk. ♂ ($\times 20$ and nat. size).

Fig. 17. *Melittobia acasta* Wlk. ♀ ($\times 20$ and nat. size).

minute pin-holes in them, were examined in November (Plate XXX, fig. 10). In most cases only one round or oval hole was present in a puparium, and this was usually situated in the middle two-thirds of the puparium though it was occasionally found at the very end; in a few two holes were found. The holes varied in diameter from 0.3 to 1 mm. Such puparia contained a dry hard mass, and some dry dusty material crowded with *Tyroglyphidae*, but a few dead chalcids of both sexes were usually present also. Very infrequently living specimens were found. Dead females were scarce, but dead males were very common, apparently indicating that many of the

¹ Mr J. Waterston is describing the anatomy of these parasites in papers to appear in *Parasitology*.

males never left the puparia in which they developed. Some of the holes seemed too small to allow the males to escape. Froggatt's observations, to be quoted later (p. 537), in regard to the relations of the sexes in another chalcid, *N. brevicornis*, are of some interest in this connection. Very rarely living chalcid larvae were found in puparia with pin-holes. The intact puparia nearly all contained the hard dry mass mentioned above and living chalcid larvae (Plate XXX, figs. 13, 15, 16), the numbers present in the large puparia varying from 17 to 41, with a mean of 27, and in the smaller puparia from 8 to 25 with a mean of 16¹. Very infrequently in such puparia dead adult chalcids were found together with living larvae. Every puparium attacked by the chalcid was found to be lined by the thick membrane, characteristic of a puparium containing a braconid larva. The chalcid was therefore in all cases a hyper-parasite. Further evidence that this was the case was afforded by dissecting the hard, dry mass mentioned above, which invariably contained a small, black, rod-like object, probably an accumulation of excrement, always present also in dissections of healthy braconid larvae. Whether this chalcid is usually a hyper-parasite or not is uncertain, for it had little or no opportunity of infecting healthy fly pupae, since the flies had emerged or were just about to emerge before the chalcid commenced its attack on the pupae. The early batch of braconids were also emerging at this time and probably escaped, but the chalcid seems to have parasitised almost every remaining pupa containing a living larva. It is capable therefore of causing an immense amount of destruction. If it is usually a hyper-parasite on the braconid larvae it is not an insect to be encouraged since it kills off large numbers of parasites very destructive to flies; if on the other hand it usually attacks fly pupae during the summer months it is most beneficial, its powers of destruction being so very great; if lastly both braconid and fly larvae are commonly parasitised, its beneficial action is somewhat neutralised. (See also p. 543.)

A fly pupa buried in the ground lies in a cavity considerably larger than itself and it seems possible that in most cases this cavity is connected with the surface by minute passages sufficiently large to admit chalcids. It may be of interest to mention that a pupa, found just below the surface of the ground on March 18, 1916, contained a number of chalcid larvae, but showed no evidence of previous parasitism

¹ Some puparia containing chalcid larvae have been kept under observation at different temperatures since November, 1915. The results obtained up to June 2, 1916 are recorded on p. 543.

by braconids. It is hoped that during the coming season opportunities may be afforded of studying more fully the habits of this interesting parasite.

Of the other species of chalcid, a *Pteromaline* which was larger than *M. acasta*, only a few specimens were found in the puparia examined in November, 1915. Eight males and twenty-four females appeared, however, between April 15–22 from eleven out of 368 intact 1914–15 winter pupae, kept to observe further developments in room B.

Chalcids are very prolific, easily reared, present no difficulties in artificial distribution, and might be utilised with great advantage in destroying fly pupae.

Table V summarises the results of the observations on 1914–15 winter pupae.

Froggatt's (1915) recently published observations on the habits of a chalcid parasite, *Nasonia brevicornis*¹, infesting the pupae of several species of blow-fly in Australia, are of great interest. He found that this parasite would attempt to deposit its eggs in larvae, but that the process took a considerable time and the creature was prevented from accomplishing its object by the movements of the larvae.

"Some fresh pupae were then placed in the tube and were quickly settled upon by the parasites, which immediately began to lay their eggs within the pupae by inserting their ovipositors through the pupal covering. Their sense of location is evidently very acute, as pupae exposed anywhere in the Laboratory were always found and attacked by parasites, which had accidentally escaped from their tubes.

"The method of ovipositing is very interesting. The female wasp spends some time crawling over and over the pupae, constantly twitching and touching them with the antennae as if searching for the least resistant spot to puncture. When this is finally decided upon, she curves the tip of the body underneath the body and inserts the point of the ovipositor. The apex of the abdomen then springs back to almost its normal position, and in so doing exposes the full length of the ovipositor, which up to this time has been hidden in a groove along the ventral plates of the abdomen.

"The body now remains motionless, except for a slight twitching of the extremity and an occasional waving of the antennae. The ovipositor is gradually inserted by what appears to be upward and downward play of the styles enclosed within the sheath.

¹ In 1911 the writer bred this parasite from the pupae of *C. erythrocephala* at Cambridge.

TABLE V. *Showing the numbers of flies, braconids and chalcids obtained from fly pupae kept under observation from October, 1914, to December, 1915.*

	"Shade tin"		Pupae transferred from "shade" to "sun tin"		"Sun tin"		Pupae transferred from "sun" to "shade tin"	
<i>Flies:</i>								
Flies emerged and caught ...	1067	(38.4 %)	17	(5.8 %)	17	(1.7 %)	1	(2.1 %)
Puparia containing fly remains ...	9	(0.3 %)	28	(9.5 %)	74	(7.6 %)	5	(10.6 %)
								12.7 %
<i>Braconids:</i>								
Braconids caught ...	1324	(50.0 %)	60	(20.5 %)	180	(18.5 %)	1	(2.1 %)
Dead braconids in puparia ...	66	(2.5 %)	4	(1.3 %)	7	(0.7 %)	1	(2.1 %)
Puparia from which braconids had emerged and escaped	304	(10.9 %)	0		0		0	
Puparia containing living braconid larvae	5	(0.2 %)	0		0		39	(82.9 %)
								87.1 %
<i>Chalcids:</i>								
Puparia with pin-holes, or containing dead adult chalcids	0		23	(7.7 %)	349	(35.9 %)	0	
Puparia containing living chalcid larvae	0		161	(54.9 %)	344	(35.4 %)	0	
								71.3 %
Other puparia ...	3		0		0		0	
Total puparia present ...	2778		293		971		47	

“When fully inserted it remains in that position for perhaps a minute, when she withdraws the ovipositor about one-half its length, and again pushes it in. This procedure may occur several times, until at last she withdraws the whole ovipositor, and it springs back to its former groove.

“The only evidence of a puncture remaining is a small bead of clear fluid at the point of insertion, but she almost immediately afterwards turns round and sucks up the liquid, and thus leaves no visible signs of her work.

“This liquid is probably used in the first case as a lubricant by bathing the styles as they work on the sheath while puncturing.

“The time occupied in the whole process of insertion and partial withdrawal and deposition of the eggs is variable, and was found to range from four to twenty-five minutes. Several attempts may be made to insert the ovipositor before deciding upon the final spot, the choice of which appears to be aided by the tactile hairs present on the apex of the abdomen.

“The eggs are white, elongate oval objects measuring .35 mm. in length and .14 mm. wide and are laid between the pupal capsule and the enclosing integument of the developing fly, the latter not being punctured by the ovipositor as might be expected. They are found associated in clusters of about ten, but sometimes groups of four and varying numbers up to and over ten may be found.

“The eggs appear to be coated with a trace of some sticky substance, which causes them to adhere together and to the covering integument of the fly pupae. The eggs remain attached to the integument during embryonic development. The young larvae hatch in about three days' time, when they measure about .3 mm. in length. They bite through the fly integument, insert the head, and while their bodies remain outside, feed upon the juices of the fly pupae.

“As the larvae develop the unfortunate pupae are gradually eaten, until the full-grown parasite larvae occupy the space occupied by the fly pupae, nothing of the latter finally remaining except the shrivelled integuments.

“The period of development of the larvae occupies about seven days from the time of hatching. The full-grown larva is a cylindrical, dirty-white, legless grub, approximately 2.4 mm. long and 1.4 mm. wide, thickest in the centre and tapering towards the extremities.

“The pupa is at first whitish in colour, with prominent eyes of reddish-brown, the legs and wings plainly visible, and the whole body enfolded in loosely-fitting skin, through which the outlines of the future perfect

insect are plainly visible. The pupa later becomes brown and then black. The pupal stage occupies about five days.

“The adults usually gnaw one hole in the puparium and escape, although two may sometimes be made.

“The time occupied from oviposition to the emergence of the adult is fifteen days, but there are indications that this varies with the temperature. The males characteristically appear a little before the females, and are active little creatures, continually running over and over the empty pupal cases. As soon as the females emerge copulation begins, the females being at once ready to receive the males.

“From each parasitised pupa both sexes may emerge, but females for the most part predominate.

“The number of parasites in each pupa varies considerably, and has been found to be as low as two, while in one instance there were as many as seventy-five, which latter batch were much smaller than the typical specimens, due no doubt to the supply of food being inadequate. In most cases, however, the number developing in a single pupa has been found to be between twenty-five and thirty-six parasites. The number of eggs laid by a single female parasite at one puncture has not been determined....The number of eggs laid by a female also seems to vary. In three instances one female placed in a tube with fifteen pupae parasitised the whole, with the exception of two pupae which had decayed. The total number developing from the one parasite in the first case was 140, in the second 148, and in the third 96.” (The numbers emerging from each pupa varied from 15 to 1 in these experiments.)

“The parasites, on the whole, are very hardy little creatures, and under careful treatment should live several weeks.”

McCarthy produced ten generations in six months and supplied thousands of parasitised pupae to various parts of the State of N.S.W. with the intention of attempting to keep down the blow-flies, which do great damage to the sheep.

CONCLUSIONS.

1. Amongst the common species of flies the very great majority of individuals pass the winter as pupae, or more rarely as larvae, which pupate early in the spring. The pupae or larvae are situated under shelter on the surface or more commonly are buried within two or three inches of the surface of the ground.

2. A very small and unimportant minority of both sexes emerging

from pupae late in the autumn or even in the winter possibly survive as adults till the spring. It is very improbable that many of these females are impregnated in the autumn, or that most of them reach sexual maturity much earlier than the broods emerging in the spring.

3. The wintering habits of *M. domestica* are still obscure.

4. The time occupied by the various stages through which a fly passes from the moment when the puparium ruptures to the time when the fly is fully formed and normally coloured varies with the temperature.

5. The majority of specimens of each species only emerge from "winter" pupae after the mean temperature of the materials in which the pupae pass the winter reaches a certain "critical" point, which differs for each species.

6. The "critical" point for *C. erythrocephala*, *F. manicata*, and *F. scalaris* seems to be about 48–50° F., and for *O. leucostoma* about 63° F.

7. In several species the majority of males emerge before the females.

8. Flies emerging from "winter" pupae seem to be the most hardy. Many of the flies of subsequent generations only live a few days, and never reach sexual maturity.

9. The estimations of the multiplication of flies during the fly season are very much exaggerated. Amongst blow-flies confined in a large open-air cage, and protected from many of their enemies and certain adverse conditions, the descendants of each female only numbered 130 individuals. Amongst "wild" flies the increase must be considerably smaller.

10. The normal duration of life amongst blow-flies is about 30 days in the summer.

11. A considerable mortality amongst flies often follows cold, wet and windy days. Oppressive sultry weather is productive of the greatest mortality. Flies die if exposed to very hot sunshine.

12. During the season many different species of flies enter rooms. It seems evident that members of most of the species enter by accident, but at least four species, *C. erythrocephala*, *S. calcitrans*, *F. canicularis* and *M. domestica* enter designedly with the intention of remaining indoors for longer or shorter periods. *C. erythrocephala* is attracted into rooms for the purpose of depositing eggs on meat. It seldom remains long indoors. *S. calcitrans* enters for shelter, and *F. canicularis* for some purpose at present unknown (p. 469). *M. domestica* remains indoors for considerable periods. Possibly in this species the development of the ova requires a high temperature, and the flies remain indoors till they are ready to deposit eggs.

13. The different species of flies vary in their seasonal distribution and in their abundance at different periods of the season. Those species which require a high "critical" temperature for emerging from pupae appear late and disappear early. The disappearance of flies in the autumn is not due to the effects of cold on the adults, but to the non-emergence of flies from pupae to replace those which are dying off.

14. The conditions, which limit the numbers of a species, are various, and up to the present have been insufficiently studied. Among the more important are the destruction of the larvae and pupae by braconid and chalcid parasites and other enemies, lack of food for the larvae, the larvae of certain species devouring those of other species, the attacks of the enemies of adult flies, and the weather and other conditions causing great numbers of freshly emerged flies of each generation to die.

15. Traps in the open baited with human excrement and decaying animal matter catch approximately equal numbers of flies. Dark receptacles in open situations usually catch smaller numbers, while traps in shady situations attract few flies. In this country it is desirable, therefore, to place all receptacles for garbage, manure and refuse in the most shady situations available.

16. Several of the species, amongst them *C. erythrocephala*, *C. vomitoria*, *F. scalaris*, *L. caesar*, and *M. stabulans*, attracted both to human excrement and decaying animal matter seldom enter rooms, and are probably of little importance as carriers of pathogenic bacteria in this country. These species, however, play an important part in spreading disease and causing discomfort under war conditions (see footnote p. 493).

17. Only about 16 % of the flies which visit human excrement and decaying animal matter are males. Males very seldom venture into dark receptacles.

18. In the case of the genus *Lucilia* very young specimens are mainly attracted to human excrement as a food, while the older specimens visit both excrement and decaying animal matter. Members of the genus *Calliphora* probably behave in the same way.

19. All the species of flies which visit excrement and decaying animal matter also visit ripe fruit, but not in the same proportions either as regards species or sexes.

20. Great contamination of fruit on trees and exposed for sale in shops with faecal and putrefactive bacteria is caused by flies and wasps.

21. The activities of flies are more influenced by temperature than by any other weather condition (p. 497). They tend to be most active in bright sunshine, are inactive in dull weather, except in the warmer months, and are very sensitive to wind, rain and great heat.

22. The larvae of *H. dentipes* and certain other species devour other fly larvae and destroy great numbers. Such carnivorous larvae must be extremely important agents in limiting the numbers of many species likely to carry pathogenic bacteria to human food.

23. The burial of carcasses does not prevent the development of the larvae present on them, or the subsequent emergence of the flies.

24. Taking into consideration the extent to which wasps visit fruit, whether on trees or exposed for sale in shops, their well-known partiality for jam and other foods, their liking for excrement, decaying animal matter and flies it seems very probable that they act not infrequently as agents in disseminating pathogenic and putrefactive bacteria.

25. Contact with infected adults of *M. domestica* is not essential in the transmission of empusa disease. *C. erythrocephala*, *H. dentipes* and *F. canicularis* occasionally die of this disease, and may be agents in transmitting it to *M. domestica*.

26. Mites of different species attach themselves to flies, and may remain clinging to them for several days. Certain observations show that they may act as carriers of nematode worms.

27. The pseudo-scorpion, *C. nodosus*, was found clinging to flies of several species, and two examples of *C. scorpoides* were found on a specimen of *S. calcitrans*. These creatures may remain attached to flies for several days.

28. The braconids, *A. manducator* and *A. cephalotes*, pass the winter as larvae in the puparia of *C. erythrocephala* and other flies. Some of the males and females of the former species emerge in the spring, but the majority do not emerge till the autumn. *A. manducator* destroys very large numbers of fly pupae, and in this respect seems to be a most beneficial parasite.

29. In these experiments a chalcid, *M. acasta*, parasitised great numbers of blow-fly puparia already containing larvae of *A. manducator*. This chalcid seems to avoid shady places. A few pupae were parasitised by other chalcids. *M. acasta* and the other chalcids hibernate as larvae in the fly puparia.

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ADDENDUM.

The following experiment, carried out under the most natural conditions possible, confirms the observations on the wintering habits of flies quoted previously. Throughout the fly season of 1915 flies were allowed to deposit their eggs on small masses of human excrement and on animal remains placed on an area of ground 6×15 feet surrounded by boards sunk vertically into the ground. In the early spring of 1916 a mosquito net cage was constructed over this area. The flies which emerged and were caught in this net could not have hibernated, but must have passed the winter as pupae, or in some cases as larvae, in the ground, under natural conditions. Several hundreds of specimens belonging to the species enumerated below emerged in the following order up to June 2: *F. scalaris*, *C. erythrocephala*, *A. radicum*, *F. canicularis*, *T. canescens*, *B. serrata*, *S. stercoraria*, *D. flaveola*, *N. cylindrica*, *P. vulgaris*, *C. vomitoria*, *H. dentipes*, *S. carnaria*, *M. lucorum*, *L. caesar*, *L. sericata*, *P. erratica*, *O. leucostoma* and *P. lardaria*.

While in 1915 only 17 flies emerged in "Tin II" (p. 443) and about 90% of the puparia were parasitised (p. 535), in 1916 (see p. 445 and Table I) from a very large number of pupae 1876 flies have appeared indicating a lesser degree of parasitism.

On Feb. 29, 1916, certain unruptured puparia, kept under observation since the autumn of 1914 and known to contain chalcid larvae, were placed in jars in rooms B and E (see p. 456). The jar in room E contained 16 puparia, each in a separate tube. On April 25 two large male pteromaline chalcids emerged from one puparium. Between May 6 and 19 *Melittobia acasta* emerged from twelve puparia, three puparia contained 2♀, another 3♀, another 5♀, another 8♀, two 10♀, another 1♂ and 1♀, two 1♂ and 5♀, and another one living ♂, two dead ♂ and 43♀. In each case after the emergence of the chalcids the puparium was carefully dissected. In four instances a few living chalcid larvae, and in one living chalcid pupae were found. All these puparia had been parasitised previously by *A. manducator*. Two of the three remaining puparia contained dead fly larvae, and the third dead chalcid larvae.

In room B, at a much lower temperature, 341 similar puparia have been kept, but up to June 2 no specimens of *M. acasta* have emerged. On that date some of the puparia were opened, and found to contain chalcid pupae.

Three puparia, containing larvae of *M. acasta*, were opened in December, 1915, and kept under observation in room B. The larvae

seldom moved, but appeared to be healthy, though exposed in the manner illustrated in Plate XXX, Fig. 15. On May 22, 1916, they passed large quantities of excrement, and had changed into pupae by May 30.

The males of *M. acasta* possess rudimentary eyes and wings, and do not seem to leave the puparia in which they develop. The females, which have well-developed compound eyes and large wings, emerge by gnawing small round holes in the puparia (Pl. XXX, Fig. 10). They were often seen to pass back into the puparia through these holes. They are very active, and live at least four weeks when confined in tubes. In one case a female gnawed a gallery 3 mm. long through the cork of a tube and escaped, and about 40 others, which were in the tube, also escaped by this means.

Females, whether obtained from puparia containing males or from puparia in which no males had developed, began to oviposit when fly pupae of various ages, both healthy and parasitised by braconids, were placed in their tubes. The process of forcing the ovipositor through the wall of a pupa sometimes occupied as long as two hours. In one instance a puparium, previously parasitised by braconids, was opened after a female had ceased ovipositing in it, and one egg was found attached to the abdomen of a pupa of *A. cephalotes*. A larva emerged in 24 hours, and developed rapidly during the next two days, remaining attached at the same spot during the whole period. From some of these puparia adults have emerged one month after eggs were deposited in them.

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